QL
1
A93
v. 2, no. 2

COMPLIMENTARY COPY

AUSTRALIAN JOURNAL OF ZOOLOGY

CORNELL UNIVERSITY
JAN 14 1955
LIBRARY

VOLUME 2
NUMBER 2
SEPTEMBER 1954

REGISTERED IN AUSTRALIA FOR TRANSMISSION BY POST AS A PERIODICAL

AUSTRALIAN JOURNAL OF ZOOLOGY

Published by the Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian National Research Council, and under the general direction of the Editorial Board (Dr. N. S. Noble (Chairman), Professor J. S. Anderson, Professor Sir Macfarlane Burnet, Professor L. H. Martin, and Professor J. G. Wood). A medium for the publication of results of original scientific research in zoology with special emphasis on the descriptive phases.

Issued as material becomes available, 7/6 per issue

EDITORIAL ADVISORY COMMITTEE

Chairman and Editor: Dr. N. S. Noble

Members: Dr. H. G. Andrewartha, Dr. A. J. Nicholson, Mr. F. N. Ratcliffe, Professor W. Stephenson, Professor H. Waring

OTHER JOURNALS PUBLISHED BY C.S.I.R.O.

Australian Journal of Physics	Issued quarterly, 30/- per annum
Australian Journal of Chemistry	
Australian Journal of Biological Sciences	
Australian Journal of Applied Science	
Australian Journal of Agricultural Research	
Australian Journal of Marine and Freshwater Research	Not issued at regular intervals, 7/6 per issue
Australian Journal of Botany	

The Organization is a signatory to the Fair Copying Declaration, details of which may be obtained from the office of the Royal Society, London.

All enquiries and manuscripts should be forwarded to:

The Editor,
Australian Journal of Zoology,
Commonwealth Scientific and Industrial Research Organization,
314 Albert Street, East Melbourne, C.2, Victoria

MELBOURNE

A FIELD STUDY ON THE BIOLOGY OF THE UNDERGROUND GRASS CATERPILLAR, *ONCOPERA FASCICULATA* (WALKER) (LEPIDOPTERA: HEPIALIDAE), IN SOUTH AUSTRALIA

By P. E. MADGE*

[*Manuscript received November* 26, 1953]

Summary

This paper describes field studies on the biology and behaviour of *Oncopera fasciculata* (Walker), an important insect pest of improved pastures in the lower south-east of South Australia and the central and western districts of Victoria.

Moths fly at dusk during September-October and mate mainly on upright grasses during these flights. The onset of flights seems to be related to a light stimulus but no correlation could be found from the data collected. Eggs are laid on the ground under pasture, where the female shelters at night and during the day; most eggs are laid within 24 hr after mating.

Larvae appear in from 3 to 5 wk and live for a short while in communities at the surface of the ground under silken webbing before building individual vertical tunnels in the soil. Larvae emerge from their tunnels along silken runways to feed on surface growth. Annual grasses and clovers are more susceptible to attack than perennials. Feeding continues from October to July and visible damage appears about May, depending upon seasonal conditions. Prepupae appear in July and pupae during July-September.

I. INTRODUCTION

During 1948-50 the indigenous underground grass caterpillar, *Oncopera fasciculata* (Walker), one of several Australian species of the Hepialidae injurious to pastures, caused severe damage to improved pastures in the lower south-east of South Australia (Fig. 1) and the central and western districts of Victoria. Larvae feed on surface pasture and thus compete with livestock for food. Feeding is most active from April to July, when food is likely to be scarce and the farmer may need all that he has to carry his livestock through the winter months. Moderate numbers of larvae in a pasture during April-July (about 6 per sq. ft.) eat new green pasture as it appears; larger numbers (10-12 per sq. ft.) eat both new green feed and old dry pasture, leaving the ground bare.

The first report of damage done by this insect in the lower south-east was in 1935; further reports of localized damage were received in 1937, 1938, and 1940. It was not until 1948, however, that severe damage took place over a wide area. This increase in numbers coincided with a great increase in the acreage of improved pastures, an intensive drainage scheme, and unusual weather. During 1951-53 the insect population was reduced to a very low level and no damage was done.

---

* Waite Agricultural Research Institute, University of Adelaide.

Before a detailed study could be made of the ecology of *O. fasciculata*, and especially the physical factors which may have contributed to the 1948-50 outbreak, information was needed regarding the life history and behaviour of this species in the field. Such information is supplied in this paper; it describes certain field observations and experiments which were done in the lower south-east of South Australia during 1950-53 and describes a laboratory experiment done at the Waite Agricultural Research Institute, Adelaide. The ecology of *O. fasciculata* will be discussed in a later paper.

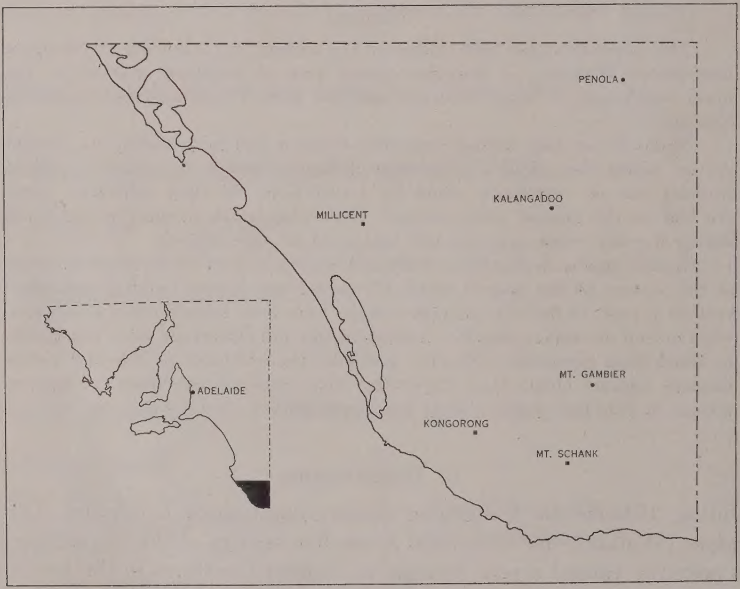


Fig. 1.—Map of County Grey, lower south-east. Inset shows southern part of South Australia with County Grey shaded.

II. Seasonal Cycle

There is a single generation of *O. fasciculata* each year (Plate 1, Fig. 1). Moths fly at dusk during the early spring (September-October) and mate during these brief evening flights. During the day, moths may be found on the ground under a protective cover of pasture. The incubation period of the eggs in the field was found to vary from 3 to 5 wk, the period being determined by temperature and humidity.

Larvae appear in the field from late September to November; most hatching occurs during late October and early November. For about a fortnight larvae shelter in communities under silken webbing among surface debris; then they make individual vertical tunnels in the soil. The remainder of the feeding stage, and the prepupal and pupal stages, are spent in these tunnels. By

December, larvae average about 0·5 in. long and have constructed vertical tunnels 1·0-1·5 in. deep; by March, they are about 1·5 in. long and are living in tunnels 3-4 in. deep. Mature larvae, in late June and early July, are 2·0-2·5 in. long and have extended their tunnels to depths of 5-7 in. Prepupae appear during July-August and, after a fortnight, pupate; this stage also lasts about a fortnight. In August the dominant stage is the prepupa, with both mature larvae and pupae present. In late September, when the main flights occur, an occasional larva may still be found.

III. Life History and Behaviour

(*a*) *Adult*

Observations on the emergence, flight, and mating of *O. fasciculata* were made during September and October 1950, on a property north-east of Mount Gambier which had been heavily infested; about one-quarter of the observation paddock was still bare of pasture. From 1951 to 1953 numbers of *O. fasciculata* on this property and elsewhere were reduced to a very low level and there was no opportunity to observe large flights.

(i) *Emergence.*—Moths were found emerging only during the afternoon. First the pupa made its way to the entrance of the tunnel and pushed through the silken cap which it had spun over the entrance as a larva. The cap was usually flush with the surface of the ground. At first the tip of the pupal head was seen; later the head and thorax were exposed. The first indication of dehiscence was the active wriggling of the pupa at the tunnel entrance. Soon the pupal cuticle split longitudinally down the dorsum and then laterally across the head and longitudinally along the ventral surface of the head and thorax. As the cuticle split, the moth underwent rhythmical convulsions which eventually freed it from the pupal case; the legs were pulled out of the pupal case and the moth then pulled itself free. The empty case usually remained in the entrance to the tunnel, the anterior portion projecting through the cap. Moths emerged in from 2 to 6 min from pupae collected in the field.

In most cases seen, the newly emerged imago remained motionless for about 5 min after leaving the pupal case, until the wings had expanded. After its wings had expanded, the moth usually spent a few minutes crawling about over the ground, apparently in search of cover. The place where it stopped appeared to be determined by a thigmotactic response; moths were seen settled against small bits of pasture or soil, although fully exposed. Upon reaching a suitable site the moth remained motionless until the time of flight and showed little or no movement when disturbed.

(ii) *Flight.*—Moths are crepuscular; they seldom fly during the day, even when disturbed. Morning flights have been seen, however, and will be discussed later. Two different types of flight were seen and will be described separately.

The first indication of an evening flight was of moths rising from the ground to a height of 20-30 ft, levelling off, and flying away until lost from sight. Some moths rose in a spiral fashion while others left the ground at an oblique angle. During this flight most moths flew singly, although an occasional pair or small group was seen; these groups were made up of a female being followed by males. During still nights moths were seen to disperse in all directions but on nights when a wind or breeze was blowing, the majority flew with the wind. Table 1 indicates the influence of wind on the direction of flights. It was difficult to determine how far the moths flew during this flight as they disappeared from view before descending. However, it appeared that the moths flew at least 50 yd and at the end of that distance gave no indication of settling down to the "hawking" type of mating flight. Moths coming into the observation area descended to about 1-2 ft above the pasture and then commenced the erratic backward and forward mating flight over the pasture.

TABLE 1

INFLUENCE OF WIND ON DIRECTION OF FLIGHT OF *O. FASCICULATA*

Date	Direction of Wind	Direction of Flight
Sept. 14	North-west	South-east
15	No wind	All directions
17	No wind	All directions
20	West	South and east
25	South	North
26	South-east	North-west
Oct. 2	No wind	All directions
9	North-west	South-east
10	North-west	South
12	South-west	North-west
14	South	North

To determine whether the "dispersal" flight was made up of adults which had emerged the same day, some newly emerged moths were collected and placed on a partially cleared position in the centre of the observation area. All seen, both males and females, on their maiden flight, flew up and away until lost from sight. Thus it appears that newly emerged adults of *O. fasciculata* probably undergo a form of dispersal flight before their mating flight.

At the same time as "dispersing" moths were seen, or more often a minute or two afterwards, other moths appeared on their mating flight. In this flight, moths rose to a height of 1-2 ft above the pasture and flew rapidly back and forth. When a large flight was at its peak a distinctive "hum" of flying moths could be heard. The usual length of flight was about 15 min. The onset of flights appeared to be related to the time of sunset; in early September they began soon after 6 p.m.; in early October after 6.30 p.m. (see Table 2). Both the beginning and end of an evening flight were abrupt, 2-3 min lapsing between the time when no moths were seen flying and full flight and between full flight and the end of flight. The looping type of flight took place over well-developed stands of pasture. Areas which were bared by *O. fasciculata* larvae were watched during several flights and it was noted that moths did not fly back and forth over these patches but flew straight across to nearby pasture; nor did large flights occur over roads or other areas where there was no pasture. During the early part of each evening flight the two sexes appeared to be in about equal numbers but as the flight continued, males became more numerous, probably because females did not return to flight after mating, but males did. The end of the flight was made up mainly of males.

During the 1950 flight period, records were kept of light intensity, surface temperature, relative humidity, and other meteorological data to determine whether there was any relationship between these physical factors and the onset of individual evening flights. The start and finish of flights were related to sunset time so that correct comparisons could be made day by day during the 1950 flight period and also with times of flights of other years. "Start of flight" means the beginning of the mating flight. The few individuals which were seen to "disperse" before the mating flight began were disregarded.

TABLE 2

METEOROLOGICAL DATA OBTAINED DURING FLIGHT PERIOD IN SEPTEMBER 1950

Date	Sunset Time	Start of Flight	Minutes After Sunset	Light Intensity (f. c.)*	Surface Temp. (°F)†	Saturation Def. (in. Hg)	Relative Humidity (%)
Sept. 12	1755	1810	15	5·25	64	0·19	68
13	1756	1810	14	3·50	68	0·17	76
15	1757	1811	14	3·50	65	0·07	88
17	1758	1814	16	1·75	66	0·21	67
20	1801	1814	13	3·50	70	0·15	79
22	1803	1812	9	3·50	64	0·17	71
23	1804	1818	14	2·62	55	0·12	73
25	1806	1821	15	2·62	53	0·09	78
26	1807	1823	16	5·25	50	0·10	72

* Obtained with photoelectric meter; candles/sq. ft. corrected to f. c.

† Obtained from thermometer on surface of ground with bulb inserted in a clump of pasture and protected from radiation.

Table 2 summarizes part of the data obtained from records of flights during September. Records of rainfall, atmospheric pressure, and wind were also kept but as these obviously had no influence on start of evening flights they were not included. Analyses of these results showed that there was no correlation between any of these physical factors and the start of evening flights. The only statement which can be made is that evening flights started about 15 min after sunset when the light intensity had dropped to near 3·5 f.c. Also, moths did not fly during heavy rains or strong winds.

Because the timing of the flights was closely related to sunset it is certain that the moths were stimulated by light. The intensity of light at certain times after sunset varied with the amount of cloud and for other causes but the correlation between light intensity and time of flight, based on nine observations, was non-significant. This may have been because there were not enough observations or because the moths were stimulated to fly by some quality of light other than its intensity. If light is the stimulus for evening flights of *O. fasciculata* a similar stimulus might occur just before dawn and the moths might be expected to fly at this time. Isolated cases of morning flights of individual moths have been recorded by other workers and observed by myself. Those seen in the lower south-east were of individual moths flying a very short distance over the pasture and then landing in cover similar to where they left. It is doubtful whether isolated morning flights have any survival value for the species. No mating occurs and it is doubtful whether they have any dispersal value because of the small number of moths which fly and the distance they cover. Any egg-laying which might take place during these brief morning flights must be of little value to the population. It seems quite certain that the appropriate light stimulus is present at the time of morning flights. The absence of mass flights and mating can probably be explained by the fact that low temperatures during the night and early morning (occasional frosts occur during September-October) lower the body temperature of the moths to the extent that they remain immobile even when stimulated to fly. The moths may vibrate their wings to raise body temperature (Krogh and Zeuthen 1941; Gunn *et al.* 1948) but even so, few would be expected to reach the "flight temperature" while the stimulus to fly was still present.

TABLE 3

INFLUENCE OF SURFACE TEMPERATURE ON FLIGHT PERIOD OF *O. FASCICULATA*

Period	Mean 9 a.m. Surface Temperature (°F)			
	Mil Lel	Eight Mile Creek	Kongorong	Kalangadoo
Sept. 10-16	63·86*	56·86	56·71	51·14
17-23	66·36**	61·43	56·28	50·54
24-30	58·50*	61·86*	59·66*	51·25
Oct. 1-7	59·92	61·20*	56·43*	50·18*

* Flights.

Duration of the flight seasons was reasonably uniform for the years studied (1950-53). Flights began early in September, reached their peak towards the end of that month, and tapered off during early October. In 1935 the flight season began about September 4 (Swan 1937).

From early September to early October, records of surface temperatures and soil temperatures at 1-, 3-, and 5-in. depths were kept at four localities in the lower south-east. Surface temperatures seemed to play an important part in determining when seasonal flights occurred, as can be seen in Table 3. Mean surface temperatures, with the flight season separated into four periods, are shown in this table. The flight season began in early September in the warmer district (Mil Lel) but did not start until early October in the coldest district (Kalangadoo). As there was no apparent relationship between seasonal flights and soil temperatures, these data have not been included. Mil Lel represents a well-drained terra rossa soil; Eight Mile Creek, a peat soil; Kongorong, a heavy terra rossa soil, and Kalangadoo, a meadow podzolic.

(iii) *Mating.*—Copulation began soon after the start of the mating flight and moths *in copula* were found during the full period of each evening flight. Males were attracted to females; as the female flew back and forth over the pasture the male crowded closely behind her, and they settled down and landed, usually on erect growth (Plate 1, Fig. 2). The male grasped the female with his genital claspers and copulation began immediately, the female clinging to the growth and the male beneath her also clinging to the growth or hanging motionless from the female. Copulation was rapid; the usual time was about 1 min. After mating, the male dropped free and rejoined the flight and the female remained clinging to the vegetation (Plate 1, Fig. 3). Males were not attracted to a female which was not flying but once she took to flight they would pursue her. Often a female would be pursued by several males and the group would land on the pasture where a male would mate with the female and the other males would flutter about the pair for a short while before rejoining the flight.

Many pairs of moths, and single males and females, were seen clinging to pasture well after dark. It is possible that moths copulating when the flight ends lose their stimulus to fly and remain clinging to the vegetation for a time before crawling down and sheltering under the surface growth.

Moths usually mated on upstanding grass or stubble but they have been found mating on the ground and on bracken fern (*Pteridium aquilinum* (L.) Kuhn).

(iv) *Oviposition.*—A female can lay eggs soon after she emerges from the pupal case, for mature eggs extend to the tips of the ovarioles, filling the abdomen and a large portion of the thorax. Although the dissection of gravid females showed that about 2000 eggs could be produced, the number of eggs laid by females in the laboratory ranged from 0 to 1500, with a mean of about 1000. Where no eggs were laid, the females were turgid with eggs.

Collections of moths during flight periods showed that few females took part in more than one flight. Occasionally tattered females were collected with most of the wing scales gone and without eggs. These females probably had flown and mated the previous evening and had laid their eggs that night or during the following day. This short oviposition period should be expected, for the adults do not feed and the small amount of fat-body the female has would be mainly expended during the mating flight.

During the flight, and for a short time afterwards, females could be heard fluttering about in the pasture. When found, they were seen laying large numbers of eggs in clumps. Many wing scales were displaced during the fluttering.

(*b*) *Egg Stage*

The normal egg, which is ovoid in shape and about 0·71 mm long and 0·52 mm wide, is white when first laid but turns a dull black within a few hours. The change of colour occurs in the endochorion; the exochorion is smooth, thin, and colourless.

In 1950 an experiment was done at the Waite Institute on the development of the eggs of *O. fasciculata* at constant temperatures. Eggs used in the experiment were obtained from moths collected in the lower south-east, 300 miles from Adelaide. Females collected during an evening's observation were sent by air mail to the Waite Institute, where they were placed in moistened pomade jars in an incubator at 12·8°C. Eggs were segregated according to moths and time of laying.

TABLE 4

DURATION OF DEVELOPMENT, PERCENTAGE DEVELOPMENT PER DAY, AND DEATH RATE AT A FAVOURABLE MOISTURE LEVEL AND SIX TEMPERATURES FOR EGGS OF *O. FASCICULATA*

Temp. (°C)	Mean Duration of Incubation Period (days)	Mean Development per Day (%)	Mortality* (%)
6·3 (±0·3)	—	—	100·0
9·8 (±0·3)	57·41 (290)†	1·75	7·9
12·8 (±0·1)	34·80 (301)	2·86	4·5
16·9 (±0·3)	19·59 (254)	5·10	7·6
20·8 (±0·2)	13·33 (288)	7·50	8·6
25·2 (±0·2)	10·97 (65)	9·13	48·0

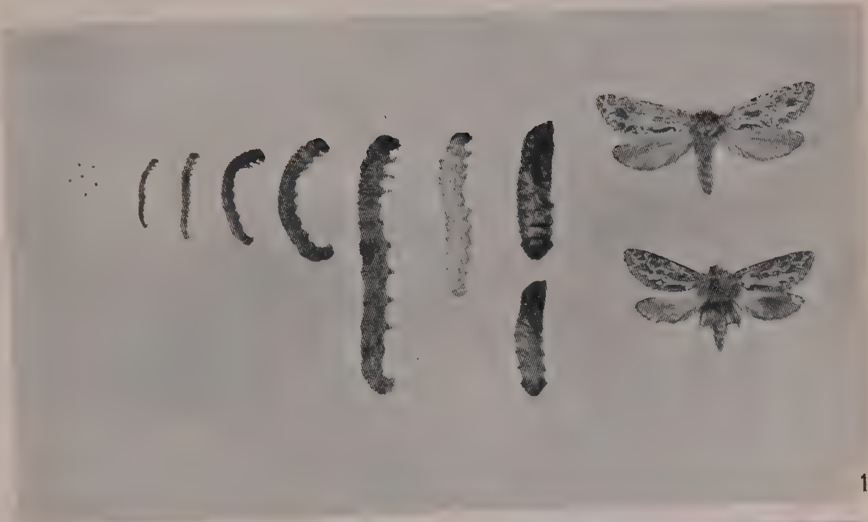
* Failed to hatch.

† Figures in brackets are the number of individuals contributing to each mean.

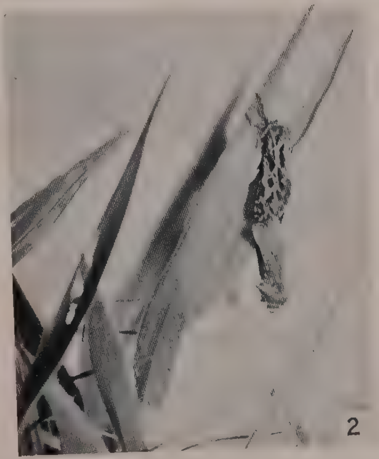
Earlier workers (Evans 1941; D. C. Swan, unpublished data; E. J. Martyn, unpublished data) have shown that *Oncopera* eggs do not hatch if they are not kept moist, and in this experiment eggs were incubated on moist filter paper in a petri dish. These were placed on glass stands in air-tight Fowler jars containing distilled water. Six constant temperatures, ranging from 6·3° to 25·2°C, were used. Temperature readings were taken each morning at 9 a.m. and the temperature of each incubator was obtained as the arithmetic mean of a large number of readings. As the eggs were in glass jars in the incubators, they would have been less exposed to temperature fluctuations than the thermometers and so would not have been subject to the fluctuations shown in Table 4.

Every 12 hr at each temperature, larvae which had emerged were counted and removed. Eggs at 6·3°C were incubated for 5 months but no larvae hatched, although a small amount of embryonic development occurred. Table 4 and Figure 2 summarize the information obtained from this experiment.

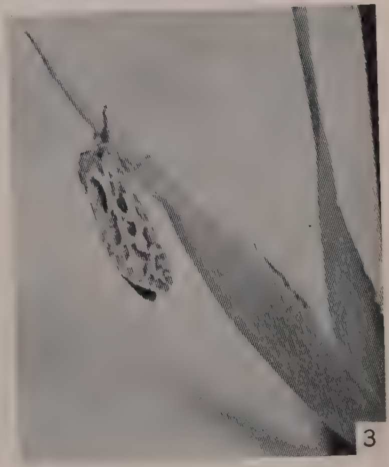
BIOLOGY OF *ONCOPERA*



1



2



3

1

2

1

2

Davidson (1944) used the calculated logistic curve to express the relationship between temperature and rate of development of insects but Browning (1952) showed that, although this curve closely followed the observed points, deviations of the points from the curve were significant. In the present experiment a freehand sigmoid curve was drawn through the observed points (Fig. 2); this is adequate for the interpolations which may be required for ecological or practical purposes.

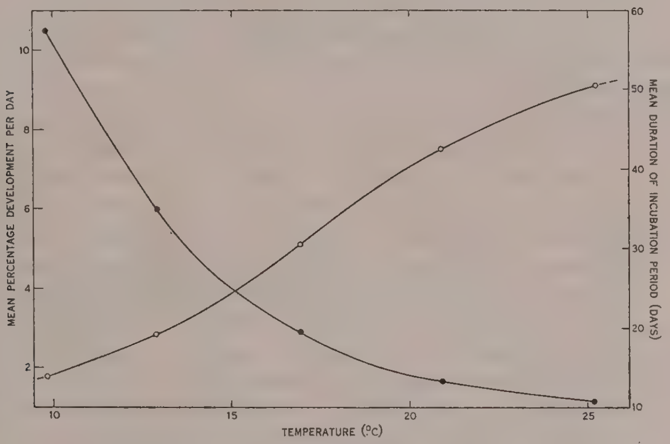


Fig. 2.—Observed points on the temperature-time curve (closed circles) and percentage development per day curve (open circles) for the eggs of *O. fasciculata*. The observed points are plotted from data given in Table 4.

(*c*) *Larval Stage*

Larvae do not have hatching spines and appear to rupture the chorion by rhythmical contractions. Some larvae split the egg shell in two. Usually, however, the empty shell retains its shape and can be distinguished from whole eggs only by being pressed, when the emergence split can be seen.

Newly emerged larvae in moist surroundings increased rapidly in size from the intake of air and moisture. When 12 hr old, larvae averaged 2·63 mm in length. The head and upper surface of the first thoracic segment were brown, the rest of the body translucent. Larvae were active and wriggled convulsively when disturbed. They did not seem to be cannibalistic in this stage; when two larvae came together both retreated rapidly.

First instar larvae, in the laboratory, crawled into the soil and spun silken shelters among the soil particles at the surface. While in this stage they apparently fed on young grass, decayed organic matter, and possibly soil, fungi, and moulds. After a week or more, they constructed individual tunnels in the soil.

When starting to tunnel, a larva forced its way head first into the soil, moving the head back and forth and pushing downward. When full length in the soil it backed out and then backed into the tunnel; then it spun a silken covering over the entrance to the tunnel and so was sheltered beneath the surface of the soil.

As the larva grew it increased the size of the tunnel by entering head first, biting off soil from the bottom and sides of the tunnel, backing out with the soil and depositing it over the covered entrance and runways. The final depth of the tunnel seemed to be determined by the ease with which a larva was able to "work" the soil; tunnels up to 9 in. long have been found in loose volcanic soils, while larvae living in heavy rendzina soils seldom made tunnels more than 4 in. deep.

Most faecal matter was deposited in a small excavated hole near the tunnel entrance, and along the surface runway.

A narrow silken strip was spun up one side of the tunnel and served as a "ladder" by which the larva crawled up and down. No silk was applied to other parts of the tunnel. This silken strip was extended horizontally along the surface of the ground and the larva crawled along it to feed (Plate 2, Figs. 1 and 2). A silken cover was built over most of the runway and portions of dry leaves, grass stems, and soil were attached, providing concealment. When the tunnel and silken runways were completed, the larva was able to leave its tunnel and crawl out along part of the runway without being seen; the silken covers did not extend the full length of the runways and the larva would be exposed while feeding. One tunnel might have from one to three runways leading away from it and some runways extended as far as 8 in. from the entrance of the tunnel. The area over which a larva could forage depended upon the number and length of these surface runways because it did not leave them. Occasionally runways were built upwards into the pasture.

Larvae fed at night, although occasionally they were found on the surface during the day. As daylight approached, they carried pieces of food to the entrances of their tunnels to be eaten during the day. Larvae cut off pasture at ground level and ate the upper portion. In areas where the larvae of *O. fasciculata* were numerous the first indication of damage was usually this "falling over" of pasture (Plate 3, Fig. 1). As feeding continued the felled pasture was entirely eaten, so that by May or June the area was completely bared of cover (Plate 3, Fig. 2). Although large numbers of larvae may be present in a particular paddock, damage to pasture does not usually become obvious until May-June, when larvae are about two-thirds grown. The type of season, as it influences growth of the pasture, largely determines when damage becomes visible.

Preference of larvae for food seemed to be determined mainly by the structure of the plants; pastures most heavily attacked were composed of annual grasses and clovers. Newly established paddocks of lucerne (*Medicago sativa*) have been severely damaged by *O. fasciculata* larvae while little or no damage has occurred after the stand has become established. Well-developed pastures of *Phalaris* appeared to suffer little damage; on the other hand, tussocks of cocksfoot (*Dactylis glomerata* L.) have been killed. Weeds in pasture such as dandelion (*Taraxacum officinale* Weber), cape-weed (*Cryptostemma calendula* (L.) Druce), bracken fern (*Pteridium aquilinum*), and thistles (*Carduus tenuiflorus* Curtis, *Cirsium lanceolatum* (L.) Scop., *Centaurea calcitrapa* (L.)) were not attacked.

(*d*) *Prepupal Stage*

Before entering the prepupal stage the mature larva ceased feeding and spun a silken cap over the entrance to its tunnel. Prepupae appeared in early July; they retained the larval shape but were creamy-white with a yellowish head. The change in colour was due to the end of feeding and the shedding of the brown larval skin; the creamy-white colour came from the fat-body. During the fortnight that the insect was in the prepupal stage the body became shortened and began to look like the pupa. The prepupa did not leave its tunnel but could move up and down in it.

(*e*) *Pupal Stage*

In about a fortnight the prepupal skin was shed and the obtect pupa appeared; it was unusually active and wriggled violently when disturbed. Having toothed ridges on some of the abdominal segments, the pupa was able to move up and down in its tunnel. The second to sixth abdominal segments were free in the female, the seventh also in the male. As with larvae and prepupae, the pupa was found head up in its tunnel. Male and female pupae could be distinguished by the fact that females were larger and had a more prominent abdomen. The pupal period lasted from a fortnight to 3 wk, when adults appeared.

IV. ACKNOWLEDGMENTS

This investigation was supported by funds from a grant by the Australian Wool Research Trust Fund.

It is a pleasure to acknowledge the interest shown by Mr. D. C. Swan, Head of the Department of Entomology, Waite Agricultural Research Institute, during the course of this work. I am greatly indebted to Dr. H. G. Andrewartha, under whose personal direction this work has been done, for his valuable advice and criticism.

Dr. T. O. Browning kindly started the incubation experiment while I was in the field. My wife gave a great deal of assistance with the preparation of the paper and also drew Figures 1 and 2.

Mrs. I. Mathison, Statistician, Waite Agricultural Research Institute, gave able help with the statistical problems. Mr. M. McKay helped with the photographing of mating moths and Mr. K. P. Phillips prepared the figures for publication.

V. REFERENCES

BROWNING, T. O. (1952).—The influence of temperature on the rate of development of insects, with special reference to the eggs of *Gryllulus commodus* Walker. *Aust. J. Sci. Res.* **5** (1): 96-111.

DAVIDSON, J. (1944).—On the relationship between temperature and rate of development of insects at constant temperatures. *J. Anim. Ecol.* **13**: 26-38.

EVANS, J. W. (1941).—Tasmanian grass-grubs. Tas. Dep. Agric. Bull. No. 22: 23 pp.

GUNN, D. L., ET AL. (1948).—Behaviour of the desert locust (*Schistocerca gregaria*) in Kenya in relation to aircraft spraying. Anti-locust Res. Centre, London, Anti-locust Bull. No. 3.

KROGH, A., and ZEUTHEN, E. (1941).—The mechanism of flight preparation in some insects. *J. Exp. Biol.* **18**: 1-10.

SWAN, D. C. (1937).—Insects and other invertebrates of economic importance in South Australia during the period July 1934 to June 1936. *J. Dep. Agric. S. Aust.* **40**: 717-31.

EXPLANATION OF PLATES 1-3

PLATE 1

Fig. 1.—Stages in development of *O. fasciculata*. Left to right: eggs; larvae in January, February, April, May, and July; prepupa; female pupa (top) and male; female moth (top) and male. Note rapid increase in size of larva from May to July. This growth corresponds with appearance of green feed. All stages are from the 1950 season and are ¾ actual size.

Fig. 2.—*O. fasciculata* moths copulating. Taken in field against white background.

Fig. 3.—Fertilized female remaining on growth after male has rejoined flight.

PLATE 2

Fig. 1.—Pasture removed to show covered runway built by *O. fasciculata* larva. The arrow indicates the entrance to the silk-covered runway which leads to the subterranean tunnel. Below the arrow is a portion of the exposed silken runway.

Fig. 2.—Cover removed, revealing silken runway and tunnel. Note faecal deposit near tunnel entrance.

PLATE 3

Fig. 1.—Pasture in the foreground has collapsed because *O. fasciculata* has cut it off at the base. Counts of larvae averaged 7 per sq. ft. Taken by D. C. Swan in May 1950.

Fig. 2.—Typical scene of patches of pasture eaten by *O. fasciculata*. Taken in July 1950 on observation paddock north-east of Mount Gambier. Note upright stubble on which the moths mate.

OBSERVATIONS ON THE ECOLOGY OF THE AUSTRALIAN FIELD CRICKET, *GRYLLULUS COMMODUS* WALKER*, IN THE FIELD

By T. O. Browning†

[*Manuscript received March* 5, 1954]

Summary

Gryllulus commodus has one generation each year, the active stages being present in summer and autumn and the eggs in winter and spring.

Crickets are found in abundance only in areas where the soil is heavy black clay. This affords shelter from desiccation to the eggs, which lose water very rapidly if exposed to dry conditions. Also in these areas there may be an abundance of food for the nymphs and adults, in the form of sown permanent pasture. Where either shelter for the eggs or food for the active stages is lacking the numbers of crickets tend to be lower.

Certain aspects of the behaviour and physiology of *G. commodus* which are important in relation to the survival and multiplication of the species are discussed.

The relative changes in the abundance of crickets in the south-eastern districts of South Australia were determined by a survey method during the period 1949-52. Evidence is presented that differences in the abundance of crickets from year to year are mainly attributable to differences in the amount and distribution of rainfall during the winter and spring, which result in differential survival of the eggs.

The history of cricket outbreaks in South Australia is traced and it is concluded that, if present trends in agricultural practices continue, future outbreaks will tend to be more severe and more widespread, although probably not more frequent.

I. Introduction

Gryllulus commodus is a herbivorous cricket indigenous to South Australia which in recent years has occasionally increased in numbers to the point where it constituted a serious economic problem.

In most of the area where *G. commodus* is abundant a change in agricultural practice, from grain cropping and grazing on natural pastures, to grazing on sown pastures, is in progress. The object of this study was to examine the ecology of *G. commodus* as it occurs in these areas and to consider how such a change in agriculture may influence the distribution and abundance of the species.

---

* The correct name of the field cricket is *Acheta commodus* (Walk.) (Gurney 1951). Since the generic name *Gryllulus* has been used in a series of previous publications it has been retained in this article.

† Waite Agricultural Research Institute, Adelaide.

II. The Life Cycle of G. commodus in South Australia

In South Australia *G. commodus* has one generation each year. The eggs hatch in late spring (about mid November) and there is a large number of nymphal instars during the summer. Towards the end of summer (late February) the first adults appear, and by the end of March adults constitute virtually the whole of the population. Following the first autumn rains the eggs are laid and within a month most of the adults die. Thus for about half the year (late autumn to early spring) only the eggs are present, whilst for the other half of the year (late spring, summer, and most of autumn) crickets are present in the active stages.

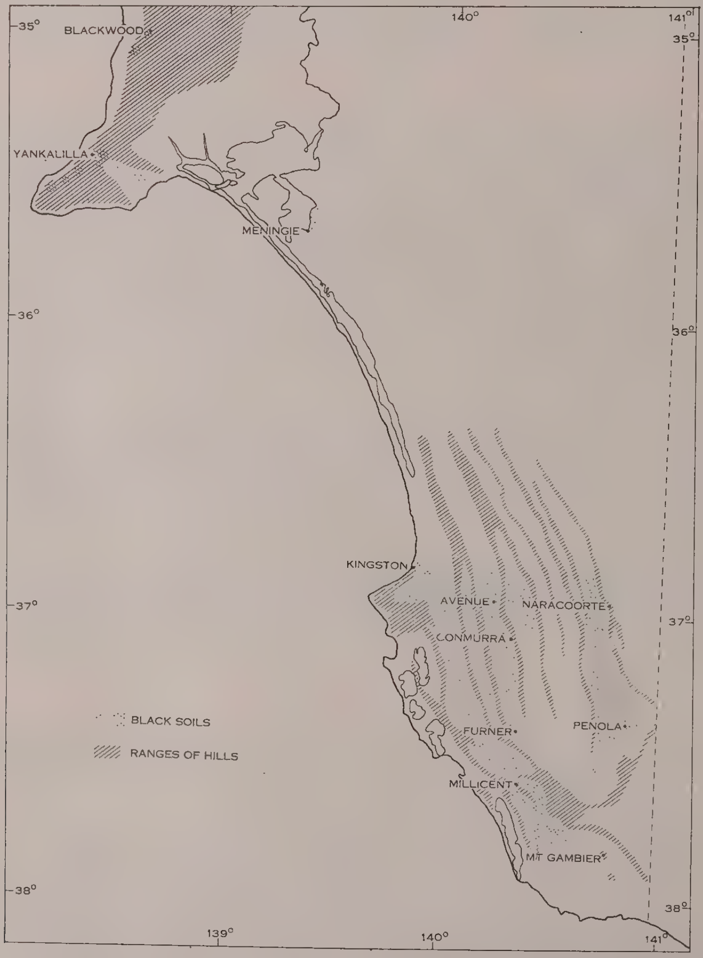


Fig. 1.—The south-eastern portion of South Australia, showing the distribution of black clay soils.

III. The Environment of G. commodus

(*a*) *Soils*

In South Australia *G. commodus* occurs extensively and in large numbers only in areas of black clay soil. It occurs much more widely than this, however, but except on this characteristic heavy black clay soil either the numbers are low or the inhabited areas are small.

Areas of black clay soil occur primarily in the south-eastern corner of the State (known as "the south-east") with a few isolated patches in the Adelaide region (Fig. 1). In the south-east black clay soils occur on flats which lie between series of low ridges which run approximately parallel to the coast (Plate 1, Fig. 2). In the Adelaide region black clays occur principally on the tops and sides of hills.

Black clay soils are characterized by a high clay content and high organic matter content and in general are derived from limestone parent material. The clay is montmorillonitic and this leads to severe cracking as the soils dry. Because they contain so much clay and organic matter such soils are able to absorb a great deal of water and so require longer periods to dry out from field capacity to the wilting point than do other soils under similar conditions.

In the south-east black clay soils vary from deep black clays which contain very little silt or salt and which tend to crumble at the surface and to crack widely when dry (Plate 1, Fig. 1) to very shallow soils, almost white in colour when dry, whose clay content is reduced and whose silt content, derived from the parent limestone, is correspondingly increased. The salt content of these latter soils is often rather high. In these soils cracking is very limited in both depth and extent. In some places no soil is present and limestone outcrops at the surface (Plate 2, Fig. 1). A continuous series of soil types intermediate between these extremes may be recognized. In general the soils tend to become shallower and lighter in texture from south to north along the flats and from inland towards the coast.

The flats on which black soils occur have very poor natural drainage (in some places the "fall" is less than 1 ft per mile (Plate 1, Fig. 2)) and, since rainfall is rather high, these areas tend to be waterlogged in winter. A system of artificial drains has done much to alleviate actual flooding but the areas are extremely wet, particularly in winters when the rainfall is above average.

In the Adelaide district black soils, which may be derived from limestone or some other parent material, occur in small areas principally on the tops and sides of hills. They are montmorillonitic clays with high organic matter contents and little silt. They are, however, not subject to flooding.

The soils which adjoin areas of black clay are of much lighter texture. In the south-east the soils of the ridges which separate the flats are consolidated shore dunes (Crocker 1941). At their southern extremities the flats adjoin areas of slightly undulating terra-rossa soils or of flat meadow podsols. At their northern ends the flats merge into the predominating sands of this region.

In the Adelaide region black soils occur as rather small patches amongst soils of the red-brown earth or podsolic types (Prescott 1944).

(*b*) *Climate*

Southern South Australia has a Mediterranean type of climate. Most of the rain falls in the winter whilst the summers tend to be arid even in the areas of higher average annual rainfall. In the hilly country near Adelaide the average rainfall is high (Fig. 2) but decreases rapidly towards the east. In the south-east the average rainfall is highest in the southernmost parts, decreasing rapidly towards the north.

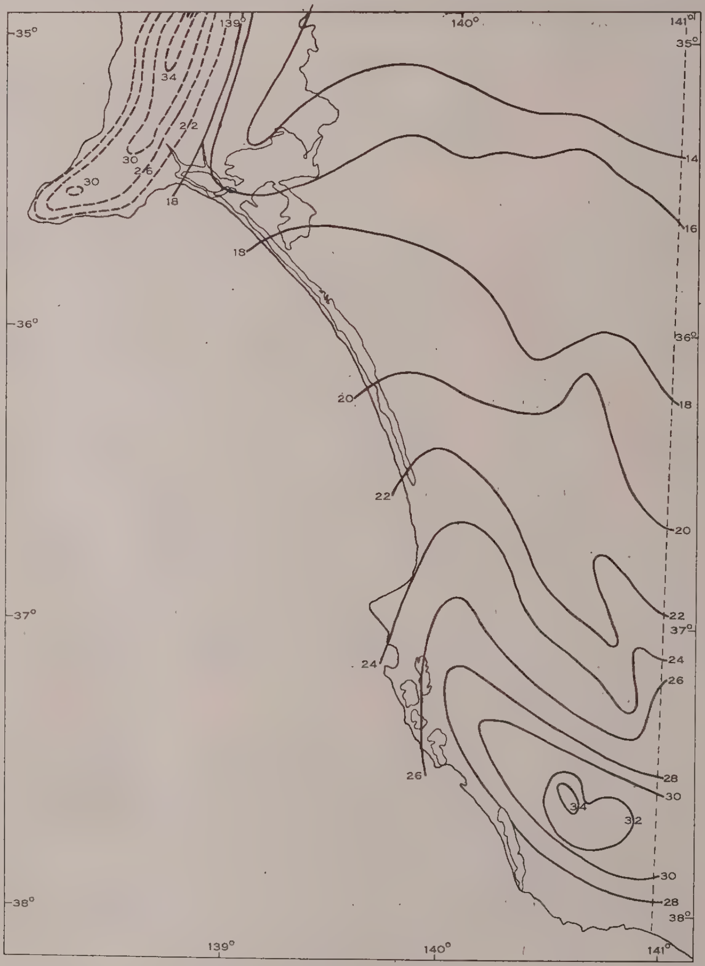


Fig. 2.—Rainfall isohyets in the south-eastern portion of South Australia. Continuous lines show isohyets at 2-in. intervals, broken lines show isohyets at 4-in. intervals.

In summer average temperatures are high over the whole of the region under consideration (mean summer temperature at Adelaide is 70·9°F) but tend to be less extreme in the southern or higher areas. In winter temperatures are mild (mean winter temperature at Adelaide is 53·1°F); few frosts occur except in the most southerly districts and in the higher lands near Adelaide.

(*c*) *Vegetation*

On the black clay soils the vegetation consists for the most part of pastures composed either of annual grasses which colonized the area following the removal of the original vegetation, or of sown, introduced grasses and legumes. There are virtually no trees in these areas except near homesteads where pines (*Pinus radiata* D.Don) are grown. In many places the native grass pastures have been top-dressed with superphosphate and this has resulted in the colonization of these areas by native legumes or introduced legumes from adjacent sown pastures.

Top-dressing with superphosphate is universally practised on sown pastures, which on black clays consist in the main of the perennials ryegrass (*Lolium perenne* L.) and strawberry clover (*Trifolium fragiferum* L.). In recent years the perennial grass *Phalaris tuberosa* L. has been used either in conjunction with, or as a substitute for, perennial ryegrass. Cropping of these soils, although widely practised in the past, has almost entirely given way to a system of permanent leys.

The areas adjoining black soils are variable in their vegetation cover, depending largely upon the soil. On the meadow podsols and red soils of the south-east permanent pastures are almost universal. Although these are "permanent pastures" they may contain many annual plants or a mixture of annuals and perennials. In many cases they are composed of annual grasses with native or introduced legumes encouraged by the use of superphosphate or they may consist of perennial ryegrass or Wimmera ryegrass (*Lolium rigidum* (Gaud.)) sown with subterranean clover (*Trifolium subterraneum* L.). On the meadow podsols and to some extent on the red soils large red gums (*Eucalyptus camaldulensis* Dehn.) form an open savannah woodland on the pastures. On the sandy soils some pasture development has been done, but for the most part the vegetation consists either of a heathland (Crocker and Tiver 1946) or a dry sclerophyll forest with stringybark (*Eucalyptus obliqua* L'Hérit.) predominating.

In the Adelaide region most of the areas adjacent to the black soils are grazed as pastures, frequently of a rather poor type, but where the soils are very sandy, as in the Yankalilla district, they retain their original dry sclerophyll forest dominated by *Eucalyptus baxteri* (Benth.) Maiden & Blakely.

(*d*) *Food Available to* G. commodus

The main source of food for *G. commodus* is green grass and the abundance of food in an area depends largely upon the state of development of the pastures. On poorer, under-developed soils food suitable for crickets is scarce. On a well-developed perennial grass and clover pasture an abundance of suitable green food is available at times when, particularly in the autumn, even the perennial native grasses have withered almost completely.

(*e*) *Other Animals Associated with* G. commodus

The most conspicuous species associated with *G. commodus* is the sheep, for both species use the same food supply. Sheep vary in their abundance from less than one sheep to the acre on undeveloped pastures to six or more to the acre on well-developed pastures. Though sheep may be numerous they are rarely allowed by the farmer to eat so much food that the crickets go short, though the converse may happen during an outbreak of crickets.

A number of species of birds prey upon *G. commodus,* of which the white ibis (*Threskiornis molucca strictipennis* (Gould)) and the magpie (*Gymnorhina tibicen leuconota* Gould) are the most important. Grey herons (*Notophoyx novaeholandiae* Latham), crows (*Corvus* spp.), and domestic fowls and turkeys also feed at times almost exclusively on crickets, judging by the composition of their faeces.

An unidentified scelionid wasp is the only known parasite of *G. commodus.* In 1949 it was found to have parasitized an average of 7 per cent. of the eggs collected at four stations in South Australia. This parasite was found in the laboratory emerging from the eggs at the same time as young crickets were hatching from healthy eggs in the same sample. There was no evidence of an extended lag in the time of emergence of the parasites compared with that of the nymphs, as occurs in *Scelio chortoicetes* Frogg. (Birch 1945). If no such lag occurs in the field adult wasps would be present 6 months before there was an opportunity to oviposit unless some alternative host is available. The wasps were not observed in the field although efforts were made to find them.

IV. The Behaviour of G. commodus in the Field

(*a*) *Behaviour in Relation to Food and Shelter*

Nymphal crickets find shelter in the cracks which develop in the black soil as it dries. It is most noticeable, when searching for crickets, that very few nymphs are to be found above ground either by day or by night even in areas where, later in the year, they are found to be most numerous. Adult crickets and crickets in their late instars tend to congregate beneath logs, stones, hay bales, lumps of cow dung, and similar objects lying on the ground, particularly if the soil is damp under them. However, during December and January, when most of the crickets are in their earlier instars, very few are to be found in such situations. Nor at this time of the year is it possible to find evidence of very much feeding. This first becomes evident along the edges of the cracks (Plate 1, Fig. 1). Later in the year damage to the pasture is much more widespread and large areas may be denuded if crickets are numerous. These observations, together with the long period required to reach the adult stage, even though temperatures are in general quite warm, suggest a form of diapause occurring in the nymphal stages.

Adult crickets spend more time on the surface of the ground than do the nymphs, and damage due to feeding becomes more severe as a greater proportion of the population reaches the adult stage. During late summer and early autumn crickets are most numerous above ground on warm sunny days and are seldom to be found during cool showery weather. Later in the season a marked change occurs in their behaviour: although not less numerous than before in fine weather the crickets are found to be most numerous above ground during light rain or after a heavy shower.

(*b*) *Behaviour in Relation to Mating and Oviposition*

It is unusual for *Gryllulus* to copulate or oviposit during the arid summer season, but a few have been observed to copulate and lay some eggs after a summer shower. However, following the first heavy autumn rains, which usually in this area mark the beginning of the rainy winter season, copulation and oviposition become general.

Females which were observed laying eggs after summer showers usually placed them in the crowns of grass plants or beside the main stems of clovers or weeds. Following the first autumn rains, however, when the top soil becomes moist, most of the eggs appear to be laid into the soil. It is likely that this behaviour is chiefly a response to the moisture content of the soil.

Table 1 shows the results of an experiment designed to test the preference of crickets, when ovipositing, for different soils and different moisture contents. Four types of soil were prepared, namely: damp sand, containing as much water as the sand would hold without excess; air-dry sand; black clay sods, containing as much water as the soil would hold without excess; and black clay sods, prepared as for the damp clods but which were subsequently desiccated in an oven until the surface became hardened and cracks appeared. The soils were arranged, in 6-in. square trays, in the form of a latin square covering the bottom of a cage in which 400 crickets were placed for 24 hr. At the end of this time the number of eggs in each tray was counted.

TABLE 1

MEAN NUMBER OF EGGS LAID DURING 24 HR IN FOUR DIFFERENT SOILS

Soil	Number of Eggs
Damp sand	1092
Dry sand	3
Damp clay	185
Dry clay	106

Difference between the means for damp and dry clay not significant. Other differences significant when $P = 0{\cdot}01$.

Most eggs were laid in damp sand. That a greater difference was not found between the damp and dry clays may be attributed to the "dry" clay still containing a relatively high proportion of water and being still relatively soft. Very few eggs were laid in the dry sand even though this, unlike very dry clay, would offer little resistance to the ovipositor.

(*c*) *Migration*

One case of migration by crickets has been inferred and other cases have been reported to me by farmers.

In March 1949, a dense population of crickets moved more or less *en masse* a distance of 6 miles from Conmurra to Avenue (see Fig. 1). The circumstances were as follows. In March a dense population of crickets occurred near Conmurra in the south-east whilst at Avenue, 6 miles further north on the same flat, no crickets could be found. In April crickets began to appear at Avenue and reached quite large numbers before they died out in mid May. At the time when crickets were appearing at Avenue food was becoming scarce at Conmurra and, although no mass movement was observed, there is little doubt that the crickets had moved from an area where they had eaten much of the available food to one where food was fairly abundant. The area between Avenue and Conmurra was at that time unimproved pasture land whereas at both Avenue and Conmurra there were sown pastures.

Farmers have reported similar observations in which the distances involved were much shorter, a matter of half a mile or so. It is usually observed that crickets move from the black flats to sandy areas near the edges of the ranges. This must result in almost complete destruction of the next generation in most years.

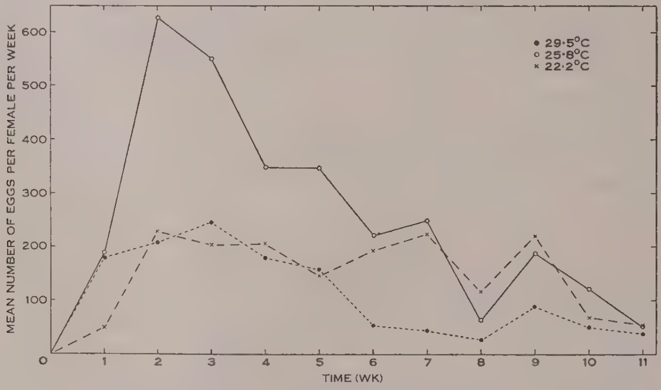


Fig. 3.—Mean numbers of eggs laid each week by crickets kept at three different constant temperatures.

V. ASPECTS OF THE PHYSIOLOGY OF G. COMMODUS OF IMPORTANCE IN INFLUENCING ITS ABUNDANCE AND DISTRIBUTION

(*a*) *Fecundity*

When individual female crickets were reared at a series of constant temperatures in the laboratory it was found that those kept at about 25°C laid more eggs than those kept at either higher or lower temperatures. In Table 2 are shown the mean total numbers of eggs laid by eight females at each of three temperatures. Figure 3 shows the mean number laid each week by the same 24 crickets.

Further analysis of the curves in Figure 3 failed to show any significant differences between any components of the egg-laying distributions at the three temperatures apart from the mean total numbers of eggs produced.

(*b*) *Diapause*

Very soon after laying, the eggs of *G. commodus* enter a state of diapause which may be rapidly completed at temperatures between 10 and 16°C (Browning 1952*b*, 1952*c*). In 1949 samples of eggs were taken from the field at Avenue, an area previously free from crickets and into which they had migrated between April 12 and May 19 of that year. A sample was taken on May 19 when no egg could have been more than 37 days old and the average age was probably less than 18 days. When these eggs were incubated at 26·8°C with no preliminary low-temperature treatment it was found that the mean duration of the incubation period was significantly greater than would have been expected from diapause-free eggs (Browning 1952*a*). In eggs from the same sample which had been stored for 15 days at 12·8°C and then incubated at 26·8°C, the mean duration of the incubation period did not differ significantly from that of diapause-free eggs (Table 3). This shows that on this occasion, diapause development had not quite been completed in the field by May 19.

TABLE 2

MEAN TOTAL NUMBER OF EGGS PRODUCED BY EIGHT FEMALE CRICKETS AT EACH OF THREE CONSTANT TEMPERATURES

Temperature (°C)	Mean Total Eggs
22·2	1597
25·8	2563
29·5	1149

Least difference for significance between means = 901 ($P = 0{\cdot}01$).

TABLE 3

MEAN DURATION OF THE INCUBATION PERIOD AT 26·8°C OF EGGS TAKEN FROM THE FIELD ON MAY 19, 1949

Treatment	Incubation Period (days)
No treatment	14·9
15 Days at 12·8°C	13·9
Diapause-free eggs (Browning 1952*a*)	13·1

On June 29, a further sample of eggs taken from the same area showed no significant difference in the duration of their incubation period regardless of whether they were stored for a period at low temperature or not. Neither did untreated eggs differ significantly from diapause-free eggs, incubated at the same temperature. The eggs had completed their diapause development within about 2 months of the time when they were laid and were competent to continue their morphogenetic development.

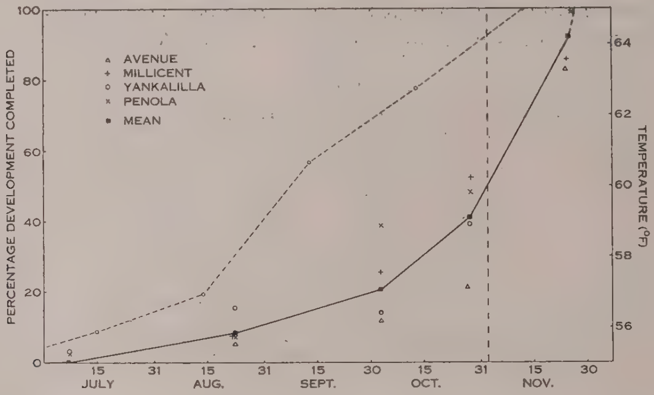


Fig. 4.—Mean percentage of development completed by eggs in the field at intervals throughout the winter and spring of 1949. The broken line shows the mean monthly maximum temperatures at Adelaide during this period.

(*c*) *Development of the Eggs in the Field*

During the winter and spring of 1949 the development of the eggs in the field was studied in the following way. Samples of eggs were taken at monthly intervals from four widely separated stations, three in the south-east and one in the Adelaide region near Yankalilla. The eggs were brought into the laboratory and incubated at a constant temperature of 26·8°C and the mean duration of the incubation period for each sample was calculated. From this figure, since the mean duration of the whole of the incubation period was known (Browning 1952*a*), the proportion of development completed by the eggs up to the time the sample was taken could be calculated. No significant differences were found between samples taken from different stations at the same time. In Figure 4 the mean proportion of development completed at each station at each sampling date is plotted against time. For comparison the mean monthly maximum temperatures at Adelaide are plotted on the same graph. It can be seen that very little development occurred during the cold winter months and that as temperatures began to rise in spring the rate of development increased. About half of the development was completed during the last month. The slow rate of development during the winter was not due to diapause, which was complete early in winter (see above), but to the prevailing low temperatures.

(*d*) *Moisture Relations of the Eggs*

Crickets are able to complete their development in extremely wet soil and they will even develop and hatch if kept submerged in water. On the other hand they have been shown to lose water very rapidly when their surroundings are not saturated with water vapour or nearly so (Browning 1953). The eggs were found to lose water most slowly during diapause and to be least resistant when newly laid and again when development was nearing completion. Even during diapause, however, the eggs lost water very rapidly when exposed to dry conditions.

VI. Distribution and Numbers of G. commodus in the South-east

(*a*) *Estimation of Numbers by Survey during* 1949-52

During the autumn of the years 1949, 1950, and 1952 a survey was made of the south-east to delimit the areas in which G. *commodus* occurred and to make an estimate of the relative numbers of crickets from place to place within these areas. The method used was to drive a motor vehicle over the area, making transects about 2 miles apart. At intervals of 2 miles along the transects the relative number of crickets in the immediate vicinity was assessed by walking about and classifying the numbers seen as either *present, few, fair numbers, large numbers,* or *swarming.* The category *present* was used when the number seen was too small to warrant the category *few* being used and in particular when no crickets were seen but males could be heard stridulating.

The whole of the black soil flats and much of the adjacent areas was covered in this way. On the densely forested ranges this was not possible and these were simply crossed at a few points. The area in the extreme south, the heathlands west of Penola, and the highlands east of Naracoorte were carefully explored but not traversed during the first year and thereafter were visited each season and rapidly examined.

The method, although arbitrary in the extreme, was found to be the only one practicable and gave results which were felt to be reasonably objective and repeatable.

Observations were not made during rainy or very cold weather, or during very strong winds, when it was found crickets tend to shelter in the cracks. The survey was left as late as possible in the year when the crickets had become adult and were thus more easily seen (see above). In 1951 the survey had just begun when the season broke with a month of almost continuously wet and windy weather and the work had to be abandoned. In 1952, owing to the pressure of other work, the survey was limited to the Avenue-Furner flat, the area round Millicent, and the area between Penola and Naracoorte. Figure 5 sets out the results of the surveys.

In 1949 crickets were numerous in the south-east but in 1950 the numbers were very low when the area is considered as a whole. By 1952 the population had increased somewhat. The few results that were obtained in 1951 indicated that the numbers of crickets were considerably higher than in 1950 but probably lower than in 1952.

(*b*) *History of Cricket Outbreaks in the South-east*

G. commodus is considered to be an indigenous insect in South Australia but, as far as can be discovered, it first occurred in numbers sufficient to cause economic loss to farmers in 1931 or 1932. Since that date serious outbreaks have occurred in 1935, 1943, and 1948.

Very little information is available concerning these outbreaks but from a report by Swan (1937); local newspaper reports, which are meagre in the extreme and often lacking altogether in years of known cricket swarms; conversations with farmers; and a little information obtained from the "remarks" column on monthly rainfall returns from stations in the south-east, it appears that the damage caused by crickets has become more severe and more widespread with each successive outbreak. Certainly the year 1948 was one in which unprecedented damage was sustained. In the remainder of this paper I shall seek to explain briefly (*a*) the observed distribution of *G. commodus*, (*b*) the fluctuations in numbers observed in recent years and what little is known about outbreaks in the past, and (*c*) the observed trend towards increasing numbers during the last two decades.

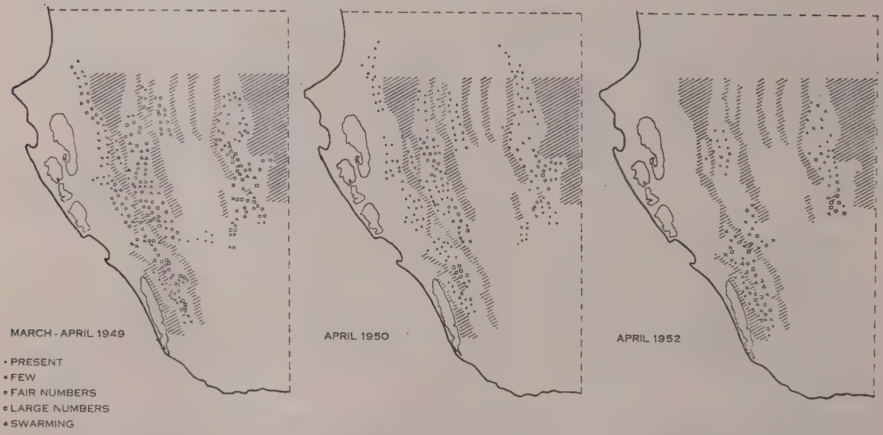
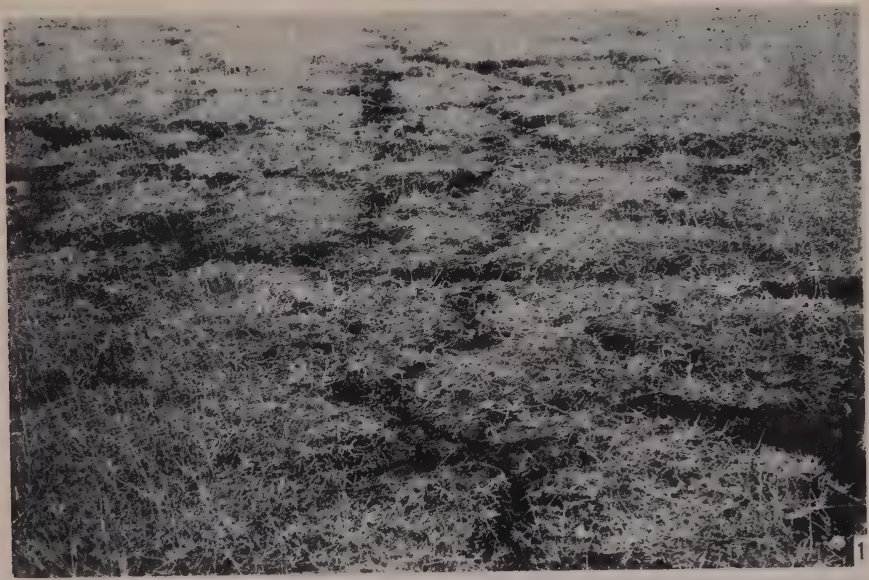


Fig. 5.—Maps of the south-east showing the relative abundance of crickets in the area as determined by survey (for explanation see text).

(*c*) *Influence of Weather*

The fall in the numbers of crickets present in the south-east in 1950 compared with the population in 1949 (Fig. 5) was very probably due mainly to the destruction of a large proportion of the eggs during the spring of 1949. During the winter and spring of 1949 eggs were sampled at intervals at four stations in South Australia (see above) and it was most noticeable that whereas eggs had been abundant during the winter they became quite scarce during a very dry period in August and September (Table 5), and by the time they were about to hatch in November they were quite scarce.



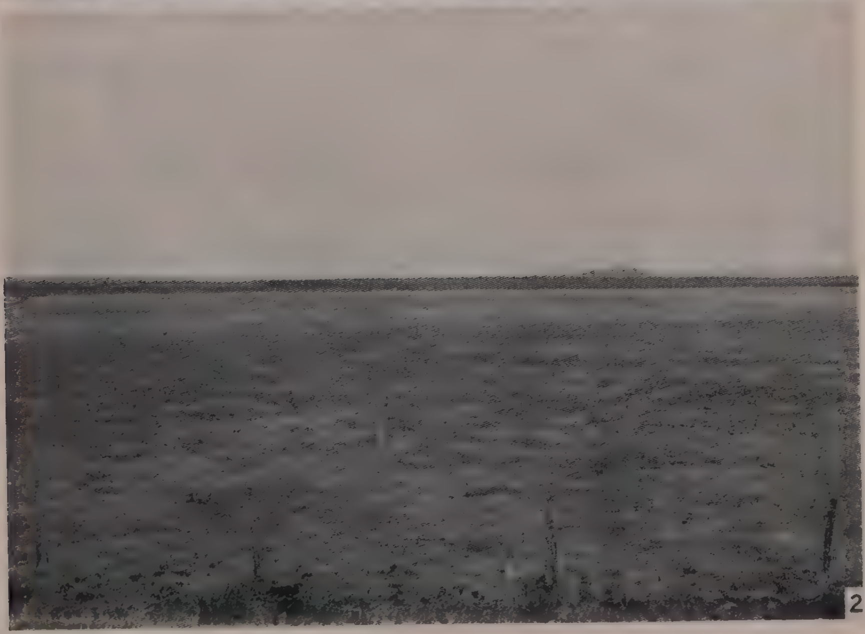
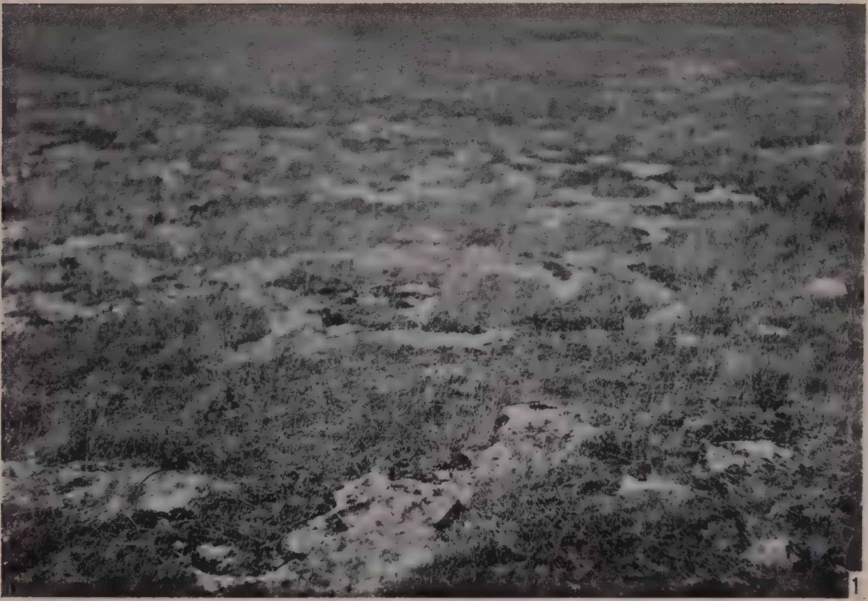
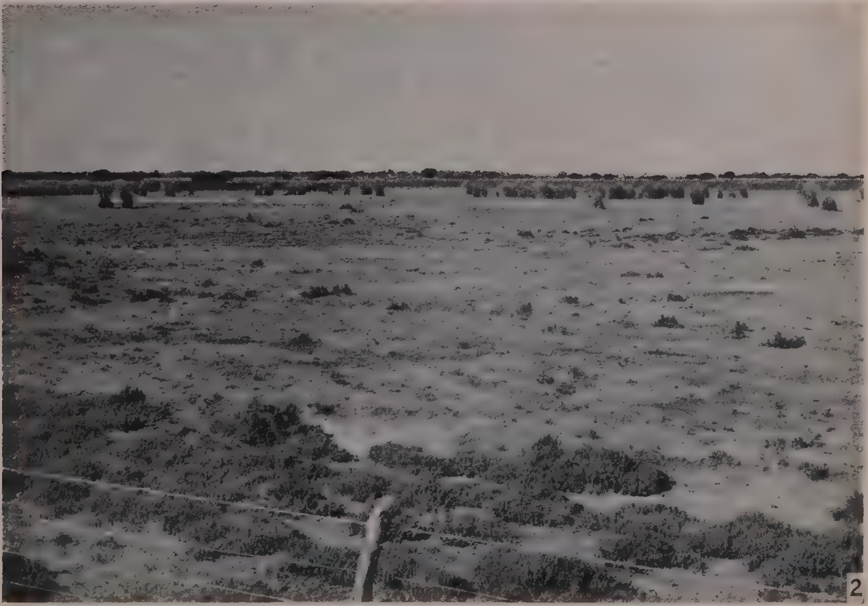


Fig. 1.—Heavy black clay soil near Millicent at the end of summer. Note how the pasture has been denuded near the edges of the cracks, owing to the feeding of crickets.

Fig. 2.—General view of the flats near Millicent, showing one of the sandy ridges in the background.



1



2

Fig. 1.—An area of black soil on which the soil is so shallow that limestone outcrops through the surface.

Fig. 2.—A typical area of unimproved black soil with very little pasture cover and clumps of cutting grass (*Gahnia trifida*) in the background.

During this dry spell the soil became very hard and the top inch or so cracked a little. It was noticeable that some of the eggs became shrunken, indicating that they had lost water. There is little doubt that the great reduction in the numbers of eggs at this time was due to their death from water loss. Dead eggs were not found in numbers, however; they are probably disposed of rapidly in the soil.

The rainfall during the winter and spring of 1950 was above average and the cricket population in the following year, although not surveyed in detail, is known to have been fairly high, which indicates a fairly high rate of survival of the eggs.

TABLE 5

MONTHLY RAINFALL TOTALS (IN.) AT ADELAIDE, AND AT MILLICENT IN THE SOUTH-EAST DURING PART OF 1948 AND 1949. FIGURES IN PARENTHESES ARE AVERAGES

	April	May	June	July	August	September	October	November
Adelaide:								
1949	2·70 (0·92)	2·38 (2·90)	1·46 (2·83)	2·81 (3·10)	1·66 (3·08)	1·42 (2·57)	6·06 (2·15)	2·52 (1·52)
Millicent:								
1948	4·13	2·80	1·94	3·86	3·65	1·74	3·02	1·57
Millicent:								
1949	0·56 (2·47)	3·53 (3·43)	1·36 (4·53)	3·38 (4·36)	1·69 (3·90)	1·33 (3·03)	4·41 (2·20)	2·68 (1·46)

In 1951 the autumn rains began in the first few days of April and rainfall was above average for the winter and spring. In the Conmurra district, however, a dry spell occurred in September and part of October when there was a period of 34 days during which only 50 points of rain fell, most of this on three consecutive days with a very light shower on one other day. During this period temperatures were fairly high in this district. Although rainfall was low in September 1951 throughout the whole of the south-east, at no other station was such a long period of drought experienced. The drought at Conmurra was less severe than that of 1949, which resulted in a great reduction in the numbers of crickets in 1950, but it is probable that it was sufficiently severe to account, in part at least, for the low numbers of crickets found in this area in 1952 (Fig. 5).

In the top graph of Figure 6 the average rainfall of the whole of the south-east (Counties Grey and Robe) is plotted for the years 1920 to 1949. The years prior to the outbreaks of 1943 and 1949 were exceptionally wet, except 1948, which was a year of average rainfall but one in which the rain was evenly distributed throughout the winter and spring (Table 5). This is not evident in the graph for the years prior to the 1930-31 or the 1935 outbreak. However, 1928 was a year of above-average rainfall at three stations on the black flats (Millicent, Naracoorte, and Penola), whilst 1929 and 1930 were also wet years at both Naracoorte and Millicent. The single report of cricket damage on which the knowledge of the 1930-31 outbreak is based came from an area between Naracoorte and Penola, and it may be inferred that the outbreak was preceded by at least one wet year.

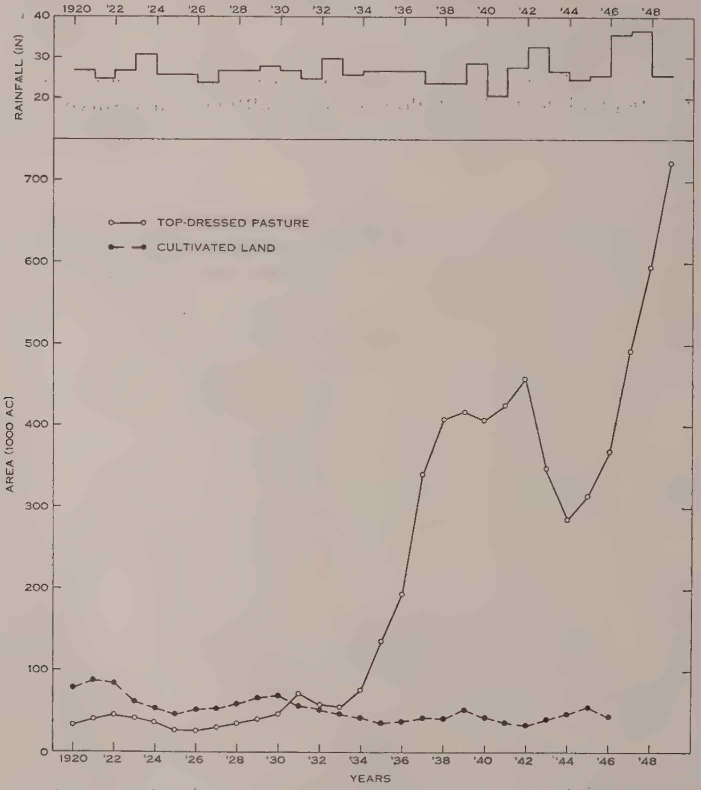


Fig. 6.—Areas of cultivated land and of pasture top-dressed with superphosphate in the south-east from 1920 to 1948. The mean annual rainfall of the south-east is shown in the top graph.

A much larger series of observations would be necessary before the correlation between wet weather and outbreaks of crickets could be stated precisely but on present evidence it seems reasonable to postulate that crickets are only likely to be numerous when the rainfall of the previous year was high.

Knowledge of the 1935 "outbreak" is also restricted to a solitary reference to crickets in the Penola district in a locality between Penola and Millicent. Rainfall recorded during 1934 in the town of Penola was below average but at Millicent, 30 miles from Penola, it was above average. This information is so indefinite that it cannot be regarded either as confirming or denying the hypothesis.

(*d*) *Influence of Soils*

Further evidence suggesting that the proportion of eggs that are killed by desiccation is the most important of the causes of changes in the abundance of crickets from year to year may be obtained from Figure 5. In each year four fairly well-defined areas were found to harbour larger numbers of crickets than others, with the exception that in 1952 the population near Conmurra was very low. That this was probably due to unusual weather in this area has been suggested above (section on weather). The map for 1950 in Figure 5 shows these four areas, near Millicent, at Furner, at Conmurra, and near Penola, very clearly. Comparison with the other years shows a similar occurrence each year, with the exception mentioned.

The soils in the four areas shown in Figure 5 are deep black clays which crack very severely and whose capacity to hold water is very high (moisture equivalents of these soils were found to be between 35 and 45). In the remainder of the south-east the black soils tend to contain a rather lower proportion of clay and a considerably greater proportion of silt and to have a generally lower capacity to retain water (moisture equivalents are generally less than 35). Such areas could be expected to provide less shelter from desiccation for cricket eggs buried in them and so to support smaller numbers of crickets than the four areas of very heavy black soil.

Cracks in the black soil provide shelter from sun, wind, and rain for nymphal and adult crickets and also serve as refuge from predacious birds. The black soils, by virtue of their capacity to retain moisture, also provide better protection for the eggs during times of drought than other soil types. It is considered that the latter is the more important aspect of shelter provided by the black soils, as evidenced by the following account of crickets in an unusual situation. In 1949 a small area, in which the soil was a deep sand, was found to be supporting fairly large numbers of crickets. This area was situated in a depression surrounded by low wooded hills and was kept moist by permanent springs. It had been sown with a mixture of strawberry clover (*Trifolium fragiferum*) and perennial ryegrass (*Lolium perenne*). Under these conditions it seems that the eggs were sheltered from droughts in winter and spring, adequate food was available for the nymphs and adults, and it may be assumed that the heavy pasture provided sufficient refuge from the birds which abounded in the scrub. It would seem that cracks, as such, do not contribute greatly to the survival of crickets.

It has not been found possible to separate the influence of soil type from that of food supply on cricket survival from a study of the crickets occurring on the black flats, for it happens that almost the only areas on which, until recently (i.e. since about 1948), any serious attempt was made to improve pastures (and consequently to provide additional food for crickets), were the same four areas of very heavy black soils mentioned above. But the importance of black soil in providing shelter (as distinct from the food associated with it) may be inferred as follows. Great areas, much greater than those on the black soils, of sown permanent pasture, providing an abundance of food suitable for crickets, occur on the red soils and meadow podsols of the south-east, but crickets are virtually absent from these areas except in special isolated instances. An adequate food supply is not then, in itself, sufficient to permit the maintenance of a large population. Some provision for the survival of the eggs, in the form of the special "shelter" provided by the black soils, also seems necessary.

(*e*) *Influence of Food*

Direct observation of the way food influences the survival and multiplication of crickets was made only in one extreme case in which the absence of an adequate food supply was observed to result in the almost complete destruction of a cricket population. In 1949, on a small isolated area of black clay soil near Adelaide, almost the whole of an initially large population was seen to die out before the first autumn rains fell towards the end of May. The extreme poverty of the pasture, which had been badly damaged by crickets in the previous year, and the absence of any green food in the area left little doubt that the disappearance of the crickets was due to starvation.

The importance of food, particularly in relation to the trend towards greater numbers during the past two decades, may be inferred as follows. Following the recognition of the necessity, in establishing permanent pastures, of growing grasses and legumes in association and of the necessity for using superphosphate as a fertilizer, the first commercial production of the seed of subterranean clover (*Trifolium subterraneum*) in 1920 (see Trumble and Donald 1938) resulted in a great increase in the area of developed pasture land in South Australia. In the south-east the increase in the area of land sown to permanent pasture did not become appreciable until about 1930, and then most of the increase, which began very abruptly (Fig. 6), occurred on the lighter, better-drained soils. On the black soils, where subterranean clover could not be grown, pastures remained in an under-developed state until about 1938, when the seed of strawberry clover (*T. fragiferum*) first became commercially available (Trumble and Donald 1941). From this date the increase in the area of sown pastures on black clay soils was rapid.

On the other hand, the area of land devoted to cropping in the south-east remained fairly steady from the turn of the century, but about 1920 a steady decline in the area under crop commenced and is still continuing. On the black flats in the four areas of very heavy soil most of the land was devoted to barley-growing until, in the third decade of this century, this practice began to give way to permanent pasture development. At the present time virtually none of this land is cropped.

The remainder of the area of black soils, which had never been farmed extensively, was devoted to grazing land on which the pasture consisted of the native plants and poor exotics which had colonized the area following the removal of the trees (*Banksia* and *Melaleuca*) and yaccas (*Xanthorrhoea*). This vegetation consisted primarily of perennial grasses such as white tussock (*Poa caespitosa* G. Forst.) and species of *Danthonia*, and sedges such as cutting grass (*Gahnia trifida* Labill.) (Plate 2, Fig. 1) and thatching grass (*Cladium filum* (Labill.) R. Br.), together with annual grasses. Even the perennial grasses wither in summer, only the crowns remaining green, and the grazing on such pastures was very poor.

During the period from 1930 to 1948 the acreage of land in the south-east devoted to improved permanent pasture has increased from 47,500 to 723,500 acres. Of this area about one-third is sown pasture and the remainder consists of cleared land on which superphosphate has been spread with the object of encouraging the growth of legumes. Since the war (1939-45) the South Australian government has been responsible for the improvement of a great deal of land for the settlement of returned soldiers and this and the consequent breaking-up of large holdings into smaller units, together with the high price for wool, have very largely contributed to the increase. A considerable proportion of this increase has occurred on black clay soils.

Prior to 1920 then, the black flats of the south-east were either devoted to barley-growing or were used for grazing in a very under-developed state. On the cultivated areas, where cropping was in most cases continuous, the soil was made quite unsuitable for the survival of cricket eggs. Ploughing was done immediately the first autumn rains had fallen, making the soil unsuitable for egg-laying. Eggs that had been laid would have had a much reduced chance of survival, for many would be buried or exposed to desiccation. On the areas devoted to grazing the amount of food available would have supported only a small cricket population. The rate of survival of eggs in these soils would have been low, as it is today. Thus it would seem that the black flats in the early part of the century were not highly suited to the maintenance of large numbers of crickets.

With the change in the system of agriculture from cropping to grazing on permanent pastures, ploughing, which was probably the greatest obstacle to cricket survival on the heavy black soils, became of diminishing importance and at the same time the pastures which took the place of the cultivated land provided a source of food for crickets. Finally, with the advent of better strains of strawberry clover, the virtual elimination of ploughing, and the gradual improvement of a proportion of the old grazing land through the use of superphosphate (if not through the sowing of pasture seed) the opportunities for the survival and multiplication of crickets were considerably increased. Even on the poorest of the clay soils the development of a dense mat of pasture would have a considerable influence on the rate of water loss from the surface of the soil. A much longer drought would be necessary before the soil moisture in the top quarter of an inch fell to the wilting point than when the soil was bare.

There is thus some evidence that the status of *G. commodus* as a pest in the south-east is a result of the present trend in agricultural practices on the black soils. Since there is no indication that the area devoted to pastures will decrease in the near future, nor that those areas at present in an undeveloped or under-developed state will not be further improved along the same general lines as are at present being practised, outbreaks of crickets might be expected to increase in severity. The area liable to be infested during an outbreak may increase because areas now marginal for the survival of crickets may be made favourable by the development of highly improved pastures. On the other hand the frequency of outbreaks may not alter appreciably since this is determined largely by the incidence of rainfall during spring.

VII. References

Birch, L. C. (1945).—Diapause in *Scelio chortoicetes* Frogg. (Scelionidae): a parasite of the eggs of *Austroicetes cruciata* Sauss. *J. Aust. Inst. Agric. Sci.* **11**: 189-90.

Browning, T. O. (1952*a*).—The influence of temperature on the rate of development of insects, with special reference to the eggs of *Gryllulus commodus* Walker. *Aust. J. Sci. Res.* B **5**: 96-111.

Browning, T. O. (1952*b*).—The influence of temperature on the completion of diapause in the eggs of *Gryllulus commodus* Walker. *Aust. J. Sci. Res.* B **5**: 112-27.

Browning, T. O. (1952*c*).—On the rate of completion of diapause development at constant temperatures in the eggs of *Gryllulus commodus* Walker. *Aust. J. Sci. Res.* B **5**: 344-53.

Browning, T. O. (1953).—The influence of temperature and moisture on the uptake and loss of water in the eggs of *Gryllulus commodus* Walker (Orthoptera-Gryllidae). *J. Exp. Biol.* **30**: 104-15.

Crocker, R. L. (1941).—Notes on the geology and physiography of the south-east of South Australia with reference to late climatic history. *Trans. Roy. Soc. S. Aust.* **65**: 103-7.

Crocker, R. L., and Tiver, N. S. (1946).—Sown pastures on the heathlands of the lower south-east. *J. Dep. Agric. S. Aust.* **49**: 493-9.

Gurney, A. B. (1951).—The names of the field and house crickets. *J. Econ. Ent.* **44**: 611.

Prescott, J. A. (1944).—A soil map of Australia. Coun. Sci. Industr. Res. Aust. Bull. No. 177: 15 pp.

Swan, D. C. (1937).—Insects and other invertebrates of economic importance in South Australia during the period July 1934 to June 1936. *J. Dep. Agric. S. Aust.* **40**: 717-31.

Trumble, H. C., and Donald, C. M. (1938).—Soil factors in relation to the distribution of subterranean clover and some alternative legumes. *J. Aust. Inst. Agric. Sci.* **4**: 206-8.

Trumble, H. C., and Donald, C. M. (1941).—Palestine strawberry clover (*Trifolium fragiferum*). *J. Aust. Inst. Agric. Sci.* **7**: 124-5.

A STUDY OF THE ECOLOGY OF THE ADULT BOGONG MOTH, *AGROTIS INFUSA* (BOISD.) (LEPIDOPTERA: NOCTUIDAE), WITH SPECIAL REFERENCE TO ITS BEHAVIOUR DURING MIGRATION AND AESTIVATION

By I. F. B. Common*

[*Manuscript received January* 25, 1954]

Contents

Summary 223
I. Introduction 224
II. The taxonomic status of *A. infusa* 225
III. The areas where moth assemblages occur .. 227
  (*a*) General 227
  (*b*) The Mt. Gingera Camp 228
  (*c*) Temporary moth camps 228
IV. Spring migrations of *A. infusa* 229
V. Fluctuations in the summer moth populations . 233
VI. Autumn migrations 237
VII. Behaviour and biology of aestivating moths 238
  (*a*) The pattern of resting moths .. 238
  (*b*) Activity during aestivation .. 241
  (*c*) Incidence of feeding during aestivation 244
  (*d*) Sex ratio of aestivating moths .. 246
  (*e*) Parasites and predators 246
  (*f*) Fat content of moths at Mt. Gingera 247
VIII. Origin of the moth populations 251
IX. Probable function of migration and aestivation in *A. infusa* 253
X. Discussion 256
XI. Acknowledgments 260
XII. References 260

Summary

Observations have been made during three summers on the ecology and behaviour of the bogong moth, *Agrotis infusa* (Boisd.) (Lepidoptera : Noctuidae), which occurs in large assemblages at altitudes above about 4000 ft in the Australian Alps. Moths of the spring generation migrate to the mountains, where they aestivate gregariously in crevices and small caves in certain rock outcrops at or near the mountain summits. Many of these moth "camps" are occupied annually from early November until early April. In the late summer and autumn, the moths migrate back to their breeding grounds.

A small proportion of the aestivating moths became intensely active for a period of about an hour just after sunset and just before sunrise each day,

---

* Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

when they indulged in a random flight over the outcrops. Activity appeared to be initiated by rapidly changing light intensity, and was accompanied by pigment migration in the eyes of the moths. Food was not sought when the moths were active, although the feeding response was sometimes elicited if they happened to settle on sugary food. However, moisture from rain or dew was apparently ingested as required.

Without exception the aestivating moths had not copulated and their ovaries were immature. Their fat-body was well developed and a series of estimations during the summer and autumn showed that the average fat content of the abdomens of males exceeded 61 per cent. and of females 51 per cent. of their dry weight.

Attacks by various predators on the aestivating moths seemed to be unimportant, but a mermithid nematode caused some mortality when its larvae emerged from parasitized moths in midsummer. This parasite appeared to be confined to the moth camps, where its life cycle has been adapted to the aestivating habit of its host.

Mature larvae of *A. infusa* were collected during the late winter and early spring of 1952 in pastures over a wide area of New South Wales. They were most abundant on heavy soils on the Western Slopes and Plains and caused serious damage to linseed crops in the north of the State and in southern Queensland. The main areas of heavy, self-mulching soils, where the large moth populations are believed to originate, have been broadly defined.

Although *A. infusa* is a multivoltine species, there is evidence that a facultative diapause occurs in the adults of the spring generation. This, together with migration, enables most of the adult population to avoid the breeding grounds during the summer, when the pastures are dominated by perennial grasses unpalatable to the larvae. The same individuals return to the breeding grounds in the late summer and autumn, when the dicotyledonous annuals upon which the larvae feed have germinated.

I. Introduction

Early in the history of European settlement in Australia, immense aggregations of the bogong moth, *Agrotis infusa* (Boisd.), were mentioned in popular accounts of the natural history of the colony. Bennett (1834) stated that the moths congregated about the granite masses of the Bogong Mountains in November, December, and January, when the aboriginal tribes gathered to feast on the moths. As the bodies of the insects were rich in fat, they probably constituted a useful supplement to the normal aboriginal diet. Bennett observed that the moths occurred abundantly only at certain masses of granite in this range, for he was unable to find them about the isolated rocks which occurred commonly in the area.

Bennett's account was largely confirmed by Scott (1873), who reported that in 1867 these moths had invaded the city of Sydney in such vast numbers that they constituted a public nuisance. Millions of the moths had apparently flown out to sea, for they littered the beaches north and south of Sydney for a distance of more than 100 miles. Helms (1890) observed bogong moths in the Snowy Mountains and amplified the earlier accounts of the aboriginal feasts. The use of these insects by certain native tribes has been mentioned more recently by Campbell (1926), McKeown (1935), and Bodenheimer (1951).

Despite popular interest in the moth assemblages and the periodic swarms of these insects in the coastal districts the function of this gregarious behaviour remained obscure. Froggatt (1900) investigated a widespread outbreak of caterpillars, which he identified as *A. infusa,* in many districts on the Tablelands, Western Slopes, and Western Plains of New South Wales. Wheat was the most important crop attacked. Later references to damage are vague and it has been generally assumed that the species is of little economic importance. Nevertheless the problem of the origin of the vast numbers of moths known to occur commonly in the mountains remained unsolved.

The present observations began in 1951 at Mt. Gingera (6092 ft) in the Australian Capital Territory. Certain aspects of the behaviour of the assembled moths, their seasonal occurrence, and mode of arrival and departure were studied in the summer of 1951-52. It was concluded (Common 1952) that the adults of the spring generation migrate in large numbers to the mountains, where they aestivate gregariously in well-defined "camps." At the end of the summer the moths again migrate, apparently back to their breeding grounds. In an attempt to determine the role of this behaviour in the ecology of the species the observations were continued in the 1952-53 season.

II. The Taxonomic Status of A. infusa

Noctua infusa was described by Boisduval (1838) whose type specimen came from Australia. In the original brief description, the hind wings were stated to be blackish brown (brun noirâtre), whereas Hampson (1903) figured under this name a male specimen with almost white hind wings, referring it to the genus *Euxoa.* He also figured a male specimen of *Agrotis spina* Guenée with blackish brown hind wings. Turner (1920) treated the latter species as a synonym of *A. infusa* (Boisd.).

Of the many hundreds of bogong moths from the mountain assemblages examined by the author none have had whitish hind wings. However, between May and early September, a series of specimens with whitish hind wings, similar to Hampson's figure of *Euxoa infusa,* were taken in mercury vapour light traps at Canberra. By mid September only occasional, worn specimens of this form occurred in the traps, whereas freshly emerged specimens of the form with dark hind wings began to come to light in numbers. The latter form was seldom if ever taken in the traps during the winter, but it was the only one collected throughout the spring and summer months.

There seems little doubt that Boisduval's name is correctly applied to the bogong moth. Hampson's (1903) statement that the form with white hind wings, which he figured as *A. infusa,* formed an article of aboriginal diet is therefore misleading. His figure of *A. spina* no doubt represents the bogong moth, and Turner (1920) was correct in stating that *A. spina* is a synonym of *A. infusa.*

From preliminary observations and experiments, it seems that specimens with white hind wings are a seasonal, possibly non-gregarious, form of *A. infusa.* This view is supported by studies of the genitalia of both forms which show no constant differences in structure.

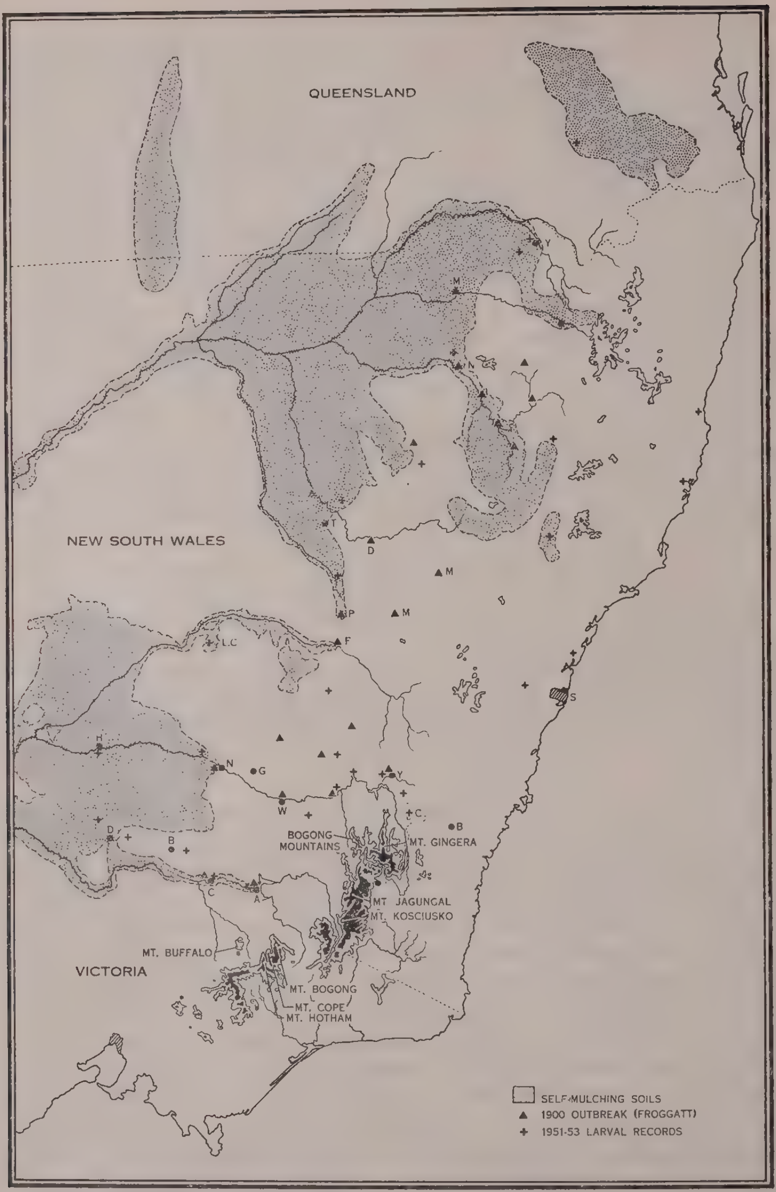


Fig. 1.—Map of south-eastern Australia showing the 3900 and 4800 ft contours, the chief areas of self-mulching soils which appear to be the most important breeding grounds of *A. infusa,* and localities where larvae have been collected either by Froggatt (1900) or between 1951 and 1953.

III. The Areas where Moth Assemblages Occur

(*a*) *General*

The mountains of the Australian Capital Territory and the Bogong Mountains form northern extensions of the Australian Alps, a series of mountains in southern New South Wales and eastern Victoria (Fig. 1). The most elevated area, the Snowy Mountains, is just north of the Victorian border and much of it exceeds 5000 ft in height, whilst numerous peaks are above the 6000-ft level. The highest point is Mt. Kosciusko, 7308 ft. The Bogong Mountains run north-west, about 20 miles west of the Brindabella and Bimberi Ranges, which form the western boundary of the A.C.T. Each of these ranges has several peaks of more than 5000 ft, and three of the highest points in the south-western part of the A.C.T. exceed 6000 ft in altitude. To the east of this mountainous area and separated from it by the broad valley of the Murrumbidgee River is the Tinderry Range which rises to a little more than 5000 ft.

The Snowy Mountains continue as the Eastern Highlands of Victoria, an elevated region much of which also exceeds 5000 ft in height. Mt. Bogong (6508 ft) is the highest point, situated at the northern end of the Bogong High Plain.

Griffith Taylor (1911) emphasized the important correlation of rainfall with contour in south-eastern Australia. In the mountains above 5000 ft the annual precipitation usually exceeds 50 in. and at 5800 ft near Charlotte Pass in the Snowy Mountains, the rainfall reaches 80 in. annually. The rainfall in the mountains also shows a marked winter incidence. Snow falls each year in areas exceeding 4000 ft in altitude and above 5000 ft often lies for three or four months each year. The prevailing winds are easterly but desiccating westerly winds frequently occur.

Pryor (1938) stated that the most important plant community in the highest parts of the A.C.T. is the *Eucalyptus niphophila* Consociation. The plant ecology of the Mt. Kosciusko area and of the Bogong High Plain has been discussed by McLuckie and Petrie (1927) and Patton (1953).

In the A.C.T., as in many other parts of the Australian Alps, the highest mountains are usually granitic. Their summits, though usually rounded, are often characterized by granite outcrops and numerous isolated granite boulders.

The largest concentrations of bogong moths appear to be associated with these outcrops. Apart from several localities in the A.C.T. (Fig. 2), aestivation camps of *A. infusa* are known or believed to occur at Mt. Jagungal (6758 ft) (Leithhead 1951) and Mt. Kosciusko in the Snowy Mountains, Mt. Bogong (4450 ft) in the Bogong Mountains (Bennett 1834), and Mt. Bogong (6508 ft), Mt. Cope (6026 ft) (B. V. Fennessy, personal communication), Mt. Hotham (6100 ft) (T. G. Campbell and C. Oke, personal communication), and Mt. Buffalo (5645 ft) (F. N. Ratcliffe, personal communication) in the Victorian Highlands. In addition, numerous other peaks are probably used by the moths. The frequent occurrence of the word Bogong in the place names of this area suggests that the moth assemblages are not uncommon.

(*b*) *The Mt. Gingera Camp*

Mt. Gingera is a high ridge, about three-quarters of a mile in length, with its axis running north-west and south-east. It is about 500 ft higher than the adjacent snow flats. The highest point of the mountain is near its south-eastern end, where large outcrops of granite rocks project in jumbled masses above the dwarfed, windswept trees. Weathering has produced innumerable deep fissures, clefts, and small caves amongst the rocks. Their surfaces are lichen-covered and often partly obscured by straggling shrubs such as *Podocarpus alpina* R. Br. and *Grevillea* sp. (Plate 1, Fig. 1). The rock outcrops are most conspicuous near the summit and on the south-western slope.

The densest concentrations of *A. infusa* moths were first observed at the summit of Mt. Gingera in January 1951. The interior surfaces of most of the crevices and small caves were covered by a single closely packed layer of moths. The floors of the larger caves were composed of a fine, silt-like material mixed with moth scales and particles of chitin. The surface layer of freshly dead moths was heavily infested with blowfly (*Calliphora* sp.) larvae. The debris, in places more than a foot in depth, represented the decomposed remains of dead moths, an indication that the camp had been occupied for a very long time. Large moth populations have now been present in these situations during four consecutive summers and probably occur there annually.

Although the largest aggregations are found in the rock outcrops near the summit, the moths also occur in suitable shelters for some distance down the south-western slope and at outcrops at the north-western end. Few moths have been observed, even in apparently suitable crevices, more than about 50 yd down the north-eastern slope. It may be significant that the other regular moth camps observed also have a westerly aspect. However, this may be determined by the availability of favourable shelters, for the largest outcrops and scree slopes in the Brindabella Range are found either at the highest points or on the western side of the mountains. Nevertheless, careful search among lesser outcrops and in scree on the eastern slopes has not revealed any moth aggregations.

(*c*) *Temporary Moth Camps*

Before the moths began to congregate at Mt. Gingera, several temporary camps were occupied at lower altitudes in the Brindabella Range. In the 1951-52 season they began to occupy the caves at Mt. Gingera at the end of October, but the following year they did not reach the summit until after November 20. By October 14, 1952, they were observed clustering gregariously during the daytime amongst rocks and debris at four sites in the Brindabella Range north of Mt. Gingera, at elevations of 4000-5200 ft. Two of these temporary camps were no more than a few yards across, but the third extended for a distance of about a quarter of a mile along the road, while the last covered an extensive area on the western slope of Mt. Little Ginini between the 5000 and 5200 ft levels.

One of the smaller camps was amongst fallen tree trunks and soil piled up beside the road when a firebreak was cleared a few months earlier. This camp had thus not been occupied previously.

The largest camp at Mt. Little Ginini was occupied by the moths throughout the 1951-52 season, but in the 1952-53 season it was used only during the spring and early summer. It extended for a distance of about half a mile along the road. The moths sheltered amongst scree for as much as 300 yd down the slope below the road and up to 50 yd up the slope above the road.

Here the moth population increased very rapidly between October 14 and 29, 1952, until all the favourable shelters amongst the loose stones and crevices were occupied. In addition most of the burnt-out hollows in tree boles and logs were lined with moths (Plate 2, Fig. 1), which were exposed to direct sunlight at various hours during the day. Early in November the population began to decline and all the moths had departed by the third week in January. The camp was not reoccupied during the remainder of the season. The other temporary camps were occupied for much shorter periods during the spring.

While this mass movement to the summits of the mountains was in progress, the moths fed freely at blossom. At dusk on October 29, in the Little Ginini camp site a few moths were observed feeding at flowers of a small *Epacris* and of a *Grevillea*. During the next fortnight moths were noticed on more than one occasion feeding after dark at *Grevillea* flowers approximately 2 miles north of Mt. Franklin at about 4500 ft. However, the numbers of moths observed feeding were not large when compared either with the immense populations present in the area, or with the numbers of moths observed feeding in October at *Eucalyptus* blossom near Braidwood and at *G. lanigera* at Canberra, at altitudes of about 2000 ft.

IV. SPRING MIGRATIONS OF A. INFUSA

According to Bennett (1834), the moths ascended from the lowlands to the mountains only during the summer months. The aborigines of the Bogong Mountain area believed that they first appeared in the lower hills and fed at the spring blossoms. They then moved up to the higher peaks, apparently as the later-flowering plants in these situations began to blossom (Scott 1873).

The periodical appearances of enormous numbers of bogong moths in the coastal areas of New South Wales prompted McKeown (1935) to state that the moths migrate from inland districts, aided in their flight by westerly winds. However, observations on directional flights by this species have only recently been reported (Common 1952).

In the spring of 1951 and 1952 large southerly flights of *A. infusa* were observed at several localities in the A.C.T. at altitudes of 2000 to over 5000 ft (Table 1 and Fig. 2). On most occasions an estimate of flight density was made by counting the number of moths passing through the vertical beam of an automobile spot light for periods of 1 min measured with a stop watch. The light produced a divergent beam effective for about 30 yd, with a diameter increasing from 7 in. 1 yd away from the light source, to 15 ft near the end of its effective range. Flight direction was determined with a prismatic compass.

On October 21, 5-7 miles east of Braidwood, N.S.W., *A. infusa* moths were observed flying west-south-west in small numbers close to the ground during

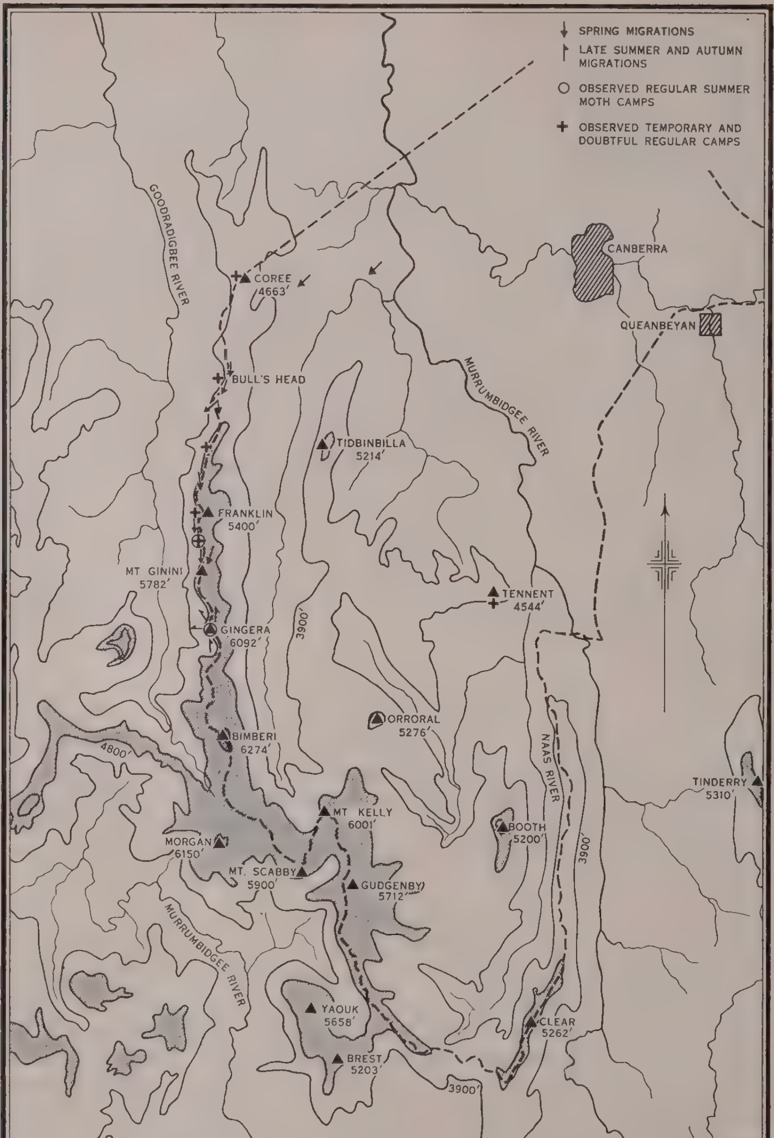


Fig. 2.—Map of the Australian Capital Territory showing the 3900 and 4800 ft contours, temporary and regular camp sites, and the directions of observed migrations of *A. infusa*. (Contours from 4 miles to 1 in. Military Map.)

the afternoon (Table 1). Simultaneously, two species of butterflies, *Pyrameis cardui kershawi* McCoy and *P. itea* Fabr., were observed migrating in the same direction. At 2.55 p.m. 68 of the former and four of the latter crossed a line 25 yd in length in 11 min. Nearby, at 3.35 p.m., one *A. infusa*, 65 *P. cardui*, 18 syrphids (*Syrphus viridiceps* Macq.), 20 thynnids (*Tachynomia adusta* Smith and *Thynnoides* sp.), and 29 ichneumonids (*Lissopimpla excelsa* (Costa) (= *semipunctata* (Kirby)) and *Echthromorpha intricatoria* (Fabr.))* crossed a line 22 yd long in 10 min, flying west-south-west.

A. infusa adults were common on October 21 near Nelligen, N.S.W., where they were flushed from their hiding places along a roadside embankment. West of Braidwood, where stringybarks (*Eucalyptus* sp.) were in full flower, moths were feeding freely in sunlight during the afternoon and, when a stick was thrown into the trees, rose in a milling swarm from the foliage. At Black Mountain, A.C.T., in late October 1951 and 1952, *A. infusa* and other species of Noctuidae were plentiful in the middle of the day and at dusk feeding at flowers of *Grevillea lanigera* A. Cunn. Adults of *A. infusa* were also common at midday feeding at flowers of *Eucalyptus* and *Xanthorrhoea australis* R. Br. 15 miles west of Canberra.

Similar reports of the moths feeding at blossom during the day were received from other centres in New South Wales and Victoria, and this behaviour is commonly observed in years when the moths are exceptionally abundant. Apiarists have then blamed the moths for severely reducing the nectar available to honey-bees (McCarthy 1945; Langridge 1952).

While the spring migrations of 1951 and 1952 were in progress, *A. infusa* adults were taken plentifully in mercury vapour light traps operated at Canberra. In 1951-52 one light trap with a low-intensity mercury vapour tube as the light source was suspended about 4 ft above the ground. In 1952-53 a second trap, with a 250-W mercury vapour discharge lamp, was placed about 30 ft above the ground. The low-intensity light trap was partially obscured by trees and a small building, but the high-intensity light trap was clearly visible from most points of the compass at a distance of more than half a mile. The latter proved to be much the more effective in recording the presence of noctuids.

In the spring of 1952, the first specimens of *A. infusa* were recorded in early September, about a month earlier than in the previous spring. Comparison of the catches in the low-intensity light trap for the two years suggests that the population of *A. infusa* in 1952 was much the greater (Fig. 3). Large catches were recorded in 1952 between early October and the end of December, the period in which the major migrations were observed and the moths were assembling in the mountains.

It is unlikely that more than one generation of adults was involved in these populations. Moths collected at blossom in late October, both in 1951 and 1952, began to lay fertile eggs in about 4 wk when fed a 2M sucrose solution in the laboratory. Furthermore, a complete generation of this species from

---

* The flies were identified by Dr. S. J. Paramonov and the wasps by Mr. E. F. Riek, both of the Division of Entomology, C.S.I.R.O.

TABLE 1

SPRING MIGRATIONS OF *A. INFUSA* IN 1951 AND 1952

Date	Locality	Altitude (ft)	Time	Weather	Flight Direction	Height of Flight	Flight Density
21.xi.1951	NE. slope of Mt. Ginini	5100	8.0 p.m.	Clear sky, wind fresh W. 12·0°C	SSW.	10-20 Ft	Well defined
14.x.1952	NE. slope of Mt. Ginini	5100	7.29-9.42 p.m.	Clear sky, light NW. breeze; 5·5°-3·0°C	Mainly S. to SW.; a few SE.	6-80 Ft	10-28 Moths per min (vertical light beam)
21.x.1952	5-7 Miles E. of Braidwood, N.S.W.	About 2000	2.55-3.46 p.m.	Scattered cloud, fresh gusty NW. to W. wind	WSW.	1-3 Ft	1-8 Moths per min per 25 yd
29.x.1952	N. slope of Mt. Ginini	5100	7.10 p.m.	Sky overcast, slight NW. wind	S.	20-60 Ft	Well defined
29.x.1952	2-2½ Miles N. of Mt. Ginini	5000	7.30-7.45 p.m.	Sky overcast, very slight NW. wind	S.	20-60 Ft, just above trees	104 Moths per min (vertical light beam)
29.x.1952	2 Miles N. of Mt. Franklin	4500	8.0 p.m.	Sky overcast; calm; light rain	10°E. of S.	20-60 Ft, just above trees	67 Moths per min (vertical light beam)
29.x.1952	1-3 Miles S. of Bull's Head	4300	8.37-8.50 p.m.	Sky overcast; calm; light rain	S. to SW.	About 60 Ft	31 Moths per min (vertical light beam)
29.x.1952	Bull's Head clearing	4480	8.55 p.m.	Sky overcast; calm; steady rain	Most S., a few SW.	20-40 Ft	117 Moths per min (vertical light beam)
29.x.1952	4 Miles E. of Mt. Coree	About 2500	9.40 p.m.	Sky overcast; calm; steady rain	SW.	20-60 Ft	7 Moths per min (vertical light beam)
29.x.1952	1 Mile SE. of Uriarra homestead	About 2000	10.05 p.m.	Sky overcast; calm; steady rain	SW.	2-8 Ft	Sparse
2.xii.1952	N. slope of Mt. Ginini	5100	9.30 p.m.	Scattered cloud; bright moonlight; light NE. breeze	S.	20-40 Ft, just above trees	Very dense stream, 500 yd wide, too many to count

the time the eggs are laid until the moths of the following generation begin to oviposit, even at 24°C, requires a period of about 7 wk. Almost without exception, adults collected in the light traps in the spring had not copulated. Their fat-bodies were well developed and their ovaries immature.

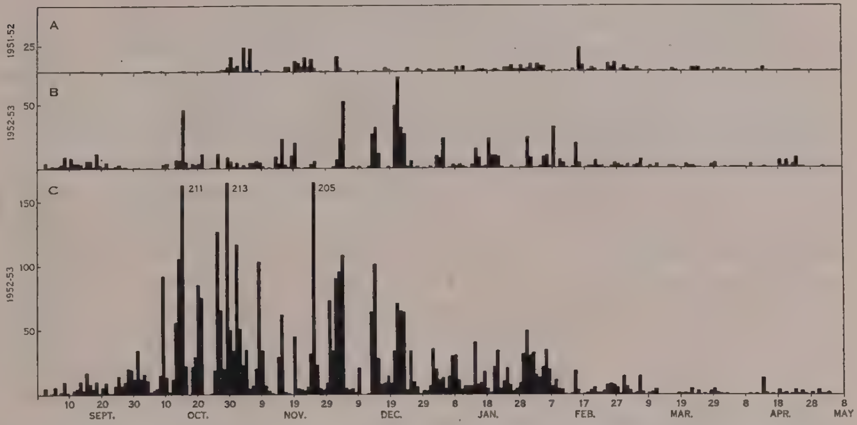


Fig. 3.—Catches of *A. infusa* in two mercury vapour light traps at Canberra, A.C.T., 1951-53. *A* and *B*, low-intensity light source in a trap about 4 ft from the ground. *C*, 250-W light source in a trap about 30 ft from the ground.

V. Fluctuations in the Summer Moth Populations

Observations on the relative magnitude of the moth population at Mt. Gingera were made at weekly intervals from November 1951 to April 1952, whereupon it became clear that the numbers did not remain constant. The occurrence of gross variations in the size of the population was determined by inspection each week (Fig. 4).

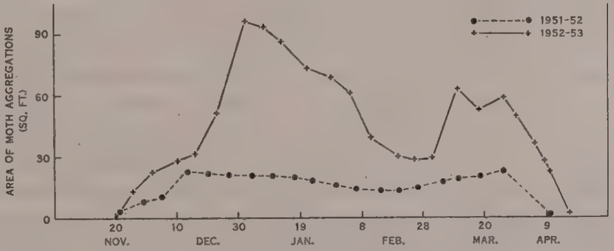


Fig. 4.—Fluctuations of *A. infusa* populations in the chief observation cave, Mt. Gingera, A.C.T.; 1951-52 and 1952-53 seasons.

The moths first began to occupy the caves at the summit at the end of October and thereafter the population increased at an irregular rate to a maximum on December 13. A slight decrease in the population may have followed during the next 4 wk. From January 10 until February 14, the decline in moth numbers was more clearly evident, when rather more than half the previous areas were covered. By February 25 an increase in the population was recorded and the numbers continued to increase until March 26, when the area occupied again approximated that at the population maximum. Between March 26 and April 10, the majority of the moths disappeared.

A more precise method was used to trace the trends in moth populations in the 1952-53 season. One of the larger caves was selected for these measurements because its roof was formed almost entirely by a single flat slab of granite which sloped at an angle of about 20° to the horizontal. The higher side was formed by an irregular mass of rocks about 2 ft 6 in. high upon which one edge of the granite slab rested. The other edge of the slab rested upon the ground. Irregular areas of the roof of this cave were covered by moths during the previous season and it was decided to measure the area they occupied at weekly intervals throughout the 1952-53 season. To facilitate access to the cave, a trench about 2 ft deep and about 18 in. wide was dug in the floor before the moths began to arrive. The roof was then divided into squares, each with a 12-in. side, by means of white waterproof ink and the plan of the roof was plotted on squared paper. Copies of this plan were used to plot the areas covered by the moths each week (Fig. 6).

In adopting this technique, it was assumed that the numbers of moths resting per unit area was constant. To test the validity of this assumption, samples of resting moths occupying a given area were counted. The sampling was done by firmly placing the mouth of a killing jar, 3½ in. in diameter, upon a flat rock surface covered by a mass of moths. Those that projected more than half way beyond the edge of the jar were then removed and the remainder killed *in situ* and counted. A series of 15 of these samples was taken on November 5 and a further series of 10 on November 26, in caves not used for regular observations. The variation between samples in the second series was reduced by adopting a refinement in the sampling technique. When the moths were imprisoned within the mouth of the jar and the projecting moths were removed, a celluloid sleeve 5 in. in diameter was slipped over the jar and its edge held firmly against the rock. By thus enclosing the neck of the jar, the latter could be removed without allowing any of the imprisoned moths to escape. The first series of samples yielded a mean of 99·1 moths (S.E. of the mean = 3·37) resting in an area of 9·6 sq. in., or 1483 moths per sq. ft. In the second series the mean was 101·1 (S.E. of the mean = 2·31) or 1513 moths per sq. ft.

The first moths were recorded in the observation cave on November 26 and the area covered gradually increased until December 16. During the next fortnight, the population increased about threefold, the peak being reached on January 1 when 96·2 sq. ft. of the rock surface was covered. This represented a population of some 144,000 moths. The areas occupied then decreased gradually until February 25, when 29·9 sq. ft. was covered, or slightly less than one-third of the maximum. By March 11 there was again a substantial increase to 63·3 sq. ft. This was followed by a slight decrease and another increase to 58·5 sq. ft. on March 26, after which it rapidly declined until all the moths had departed by April 22 (Fig. 4).

Although the fluctuations were much more conspicuous in the 1952-53 season, when the moths were also much more numerous than in the previous season, the population in both seasons followed a similar trend.

The spring increase in population appears to have been due entirely to the arrival of the migrating moths. Various factors were probably involved in the summer decline in moth numbers. Mortality played an important part and appeared to be much less significant in the 1951-52 season than in either the 1950-51 or the 1952-53 seasons. Some mortality, due to parasitism, coincided with the main period of population decline in January and early February. However, this was also a period of high temperatures and a considerable mortality may have been caused by adverse physical factors, especially in moths occupying the less favourable situations.

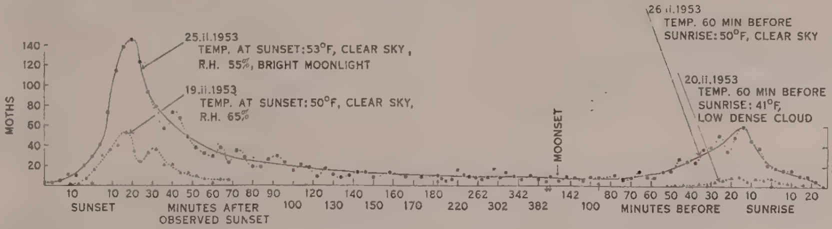


Fig. 5.—Activity determined by counting the numbers of moths in 10 observation squares (see later section) on the evening of February 19 and the morning of February 20, 1953, and throughout the night of February 25-26, 1953, Mt. Gingera, A.C.T.

The more rapid decline in the population, recorded in February 1953, was largely attributed to a movement of moths away from Mt. Gingera. On February 4, just after sunset, numerous moths were observed flying in a northerly direction at two points north and north-north-east from the summit of the mountain and at an altitude of 5500 ft. Some of the moths settled along the edges of a small stream to drink, but the majority maintained the steady northerly flight. The same evening numerous moths were observed drinking at several pools and wet areas on the road, up to 4 miles north of Mt. Gingera. Drinking moths had already been noticed at these sites on January 29, but no directional flight was noticed. No large-scale movement of moths to water was observed earlier in the season.

A northerly migration of low magnitude had therefore begun as early as February 4 and possibly even as much as a week before. The dispersal apparently continued during the next 3-4 wk, resulting in a considerable depletion of the population at Mt. Gingera. This movement away from the mountains was perhaps reflected in the increased catches of *A. infusa* recorded in the Canberra light traps about this time (Fig. 3).

On February 13 this process of population depletion was recorded photographically in one of the observation caves. A group of moths at the margin of the mass was photographed at 4 p.m. before there was any sign of moth activity, and again at irregular intervals while the evening flight was in progress (Plate 4). Evidently there was a substantial reduction in the population.

TABLE 2
AUTUMN MIGRATIONS OF *A. INFUSA* IN 1952 AND 1953

Date	Locality	Altitude (ft.)	Time	Weather	Flight Direction	Height of Flight	Flight Density
11.iv.1952	1 Mile NE. of Mt. Gingera summit	5500	6.38 p.m.	Clear sky, light W. wind	Most N.-NW. few NNE.	6-15 Ft	13-27 Moths per min (vertical light beam)
30.iii.1953	½ Mile NNE. of Mt. Gingera summit	5500	6.50 p.m.	Strong cold W. wind, with counter wind from E.	N.	2-8 Ft	Well defined
1.iv.1953	½ Mile W. of Mt. Gingera summit	5600	6.45 p.m.	Clear sky, breeze from W.	(*a*) N. (*b*) W.	(*a*) 4 Ft (*b*) 12-20 Ft	(*a*) Dense stream (*b*) Sparse stream
8.iv.1953	Mt. Gingera	6092	6.10 p.m.	Sky overcast, calm, rain threatening, 6·7°C	10° E. of N.	2-10 Ft	Dense stream
10.iv.1953	Mt. Gingera	6092	From 5.58 p.m.	Sky overcast, light rain, slight N. breeze, 9·9°C	(*a*) 10°-20° E. of N. (*b*) N. (*c*) NW.	6-20 Ft	(*a*) Dense stream (*b*), (*c*) Fairly dense streams
16.iv.1953	Mt. Gingera	6092	From 5.40 p.m.	Strong SW. wind	NNW. on leeward side of summit	10-20 Ft	Very dense stream

The increase in the population at the end of February and in March was attributed to a temporary influx of moths migrating north from the mountains farther south. Throughout the night of February 25, moth activity at the summit of Mt. Gingera was maintained by vast numbers of moths which continued to arrive from the south (Fig. 5). At the extreme south-eastern end of the mountain, a continuous stream of moths flew steadily towards the summit at a height of 2-12 ft above the ground. There was a slight westerly breeze blowing and the moon shone brightly in a clear sky until it set at about 3 a.m. As they reached the caves most of the moths entered immediately and joined the masses already there. Those that had arrived during the night rested with their bodies at an angle to those of the remainder and by sunrise formed a clearly defined band up to 5 in. wide. By March 3, most of the moths in this band had again disappeared, but on March 11 another enormous increase in the population was apparent. A further reduction and a subsequent increase during the next 2 wk suggest that the Mt. Gingera camp was being used freely as a temporary camp by moths migrating north from the mountains farther south. Simultaneously moths that had aestivated at Mt. Gingera were probably continuing to disperse.

By the end of March the departure rate apparently once more exceeded the rate of arrival and the population at Mt. Gingera rapidly declined. Mortality in the caves during the periods of late summer increase and autumn decline was at a very low level.

VI. Autumn Migrations

Apart from the evidence already given that a northerly migration had begun in early February and continued during March, direct observations on directional flights were made in early April when the population was declining rapidly (Table 2).

On March 30 there was a strong westerly wind blowing, but at the observation site the topography caused a counter wind to blow in from the east. Many of the migrating moths settled to drink at the edges of a small stream. On April 1 there were two components in the direction of flight. The greater number of moths was flying north, while another smaller stream was moving west. After the normal flight period, the directional flights ceased. On April 5 a strong, very cold westerly wind was blowing and no migrating moths were noticed.

On the evening of April 8, weather conditions were especially favourable. The first moths began to leave their shelters at 5.53 p.m. and, while only a few moths were in the air, the flight behaviour of each individual could be followed. Each moth flew with an unsteady, rather jerky motion, gradually rising in the air in spiral fashion to a height of some 30-40 ft above the summit. Still with a somewhat jerky flight, it then moved steadily away from the summit in a direction between north and 10° east of north. Its flight gradually increased in altitude as it passed beyond sight. Dozens of individual moths were seen to behave in this way during the next 15 min. Most of those rising from the western side of the summit also left the mountain in a northerly direction, but a few flew off about 5-10° north of west. A little later, when the flight was nearing its peak, a dense stream of moths was noticed leaving the camp and flying close to the ground.

The dispersal was again observed on April 10, but a slight northerly breeze made it more difficult to follow the behaviour of individual moths. Most of the moths flew in a similar jerky manner when they first left the caves. They gradually flew into the breeze away from the summit, although some were blown back several times before progress was made. At 5.58 p.m. a steady stream of moths was moving up the slope at the south-eastern end of the mountain flying 10° east of north. About 200 yd north of the summit, there was a very dense flight of moths a few minutes later moving 10-20° east of north. Two components were noticed in the direction of flight 400 yd north-west of the summit, one north-west and the other north.

The evening flights at the summit of Mt. Gingera on April 8 and 10 were probably more intense than any previously witnessed. On both occasions when the flight period ended, no further directional flight was observed in the vicinity of Mt. Gingera or on the road north.

It seems clear therefore that the rapid decline in moth numbers during the first half of April in both seasons was due to migration. The main components in the direction of movement ranged from west to north-north-east.

VII. Behaviour and Biology of Aestivating Moths

(*a*) *The Pattern of Resting Moths*

In the 1951-52 season the first moths to arrive at Mt. Gingera were observed in deep crevices in the largest caves, and the same crevices were also the first to be occupied in the 1952-53 season. These crevices were about 2 in. wide, were very dark, and probably showed the least fluctuations in temperature and humidity. The first small groups of moths formed the nuclei of the later aggregations. Those that arrived later gradually extended the first groups beyond the small crevices and into the body of the caves, where the physical conditions of light, temperature, and humidity were probably less favourable. By January 1953 the moths extended in a continuous, imbricated layer to beyond the cave entrances where, during the afternoon, many were in direct sunlight (Plate 1, Fig. 2). Even the darker side of a thermohygrograph in one of the caves was covered by moths (Plate 2, Fig. 2).

Each moth rests with its fore tarsi gripping the rock surface and its mid and hind legs on the backs of the moths behind (Plate 4, Fig. 1). A small cluster in the middle of a large surface assumes a rosetted form with the heads of most of the moths directed towards the centre of the group. Moths that join the cluster later thrust the anterior part of their bodies beneath the abdomens and wings of the moths before them. They thus maintain physical contact with their neighbours, and their light-sensitive eyes are in a relatively dark situation. In such compact formations, the individuals are probably able to resist desiccation much more effectively than are isolated moths.

The moths appear to show a preference for the darker caves and crevices, but this may be a response to physical stimuli other than light. Within caves the temperature is generally more uniform and the humidity higher than without (Geiger 1950) and, as the moths enter the caves during the night, their entry may be a temperature response. On moonlight nights at least, however, the movement into the caves may be partly determined by a negative phototaxis. Again, olfactory stimuli may operate, for caves previously inhabited by the moths have a characteristic musty odour. However favourable in other respects, wet rock surfaces are usually avoided.

If a stick is thrust into a mass of moths, not only those that have been touched but many of those in the immediate vicinity drop to the ground. The wave of disturbance spreads rapidly from the centre. The rate at which the moths drop then gradually declines. Those at the edge of the cleared space re-orient themselves by thrusting their heads as best they can beneath their neighbours. Those that have fallen quickly seek shelter, either by crawling beneath pieces of loose stone or by crawling back up the rock surface, where they rejoin the mass. At higher temperatures some of the disturbed moths commonly take to flight.

The moths that have been thus disturbed deposit drops of excrement. At the beginning of the aestivation period this has a sweet odour, but towards the end of the summer the breakdown products in the excrement make it particularly offensive. The quantity of excrement deposited varies considerably during the summer, but appears to be correlated with the availability of moisture. At the end of a dry period of 2-3 wk, the moths scarcely excrete at all when disturbed.

Many of the moths in the caves appear to remain in a more or less quiescent state for periods of several weeks. Evidence was obtained, by plotting the areas covered from week to week on the roof of one of the largest caves, that only minor changes in the disposition of many of the moths occurred between January 1 and March 3, 1953 (Fig. 6). The population gradually declined during this period, but the depletion followed a definite pattern. For the first fortnight, only the moths in the most exposed positions at the entrance to the cave disappeared. Then simultaneously with this marginal recession, small numbers of moths began to drop out elsewhere, leaving a series of irregular unoccupied spaces. During the succeeding weeks, these spaces grew in size until adjacent ones became confluent. As this process continued, the unoccupied spaces became so large that there remained only a series of irregularly shaped bands of moths extending over the roof, until they in turn gradually broke up and shrank towards the margins of the cave. A wet but otherwise favourable area of the roof at the rear of the cave, which was avoided by the moths when the cave was occupied initially, remained bare, even after it had dried in early January. However, when the population again suddenly increased between March 3 and 11, most of this unoccupied area was covered with moths. Throughout this period of about 9 wk, there was no general re-shuffle of the population, which would certainly have occurred had most of the moths been active at any one time.

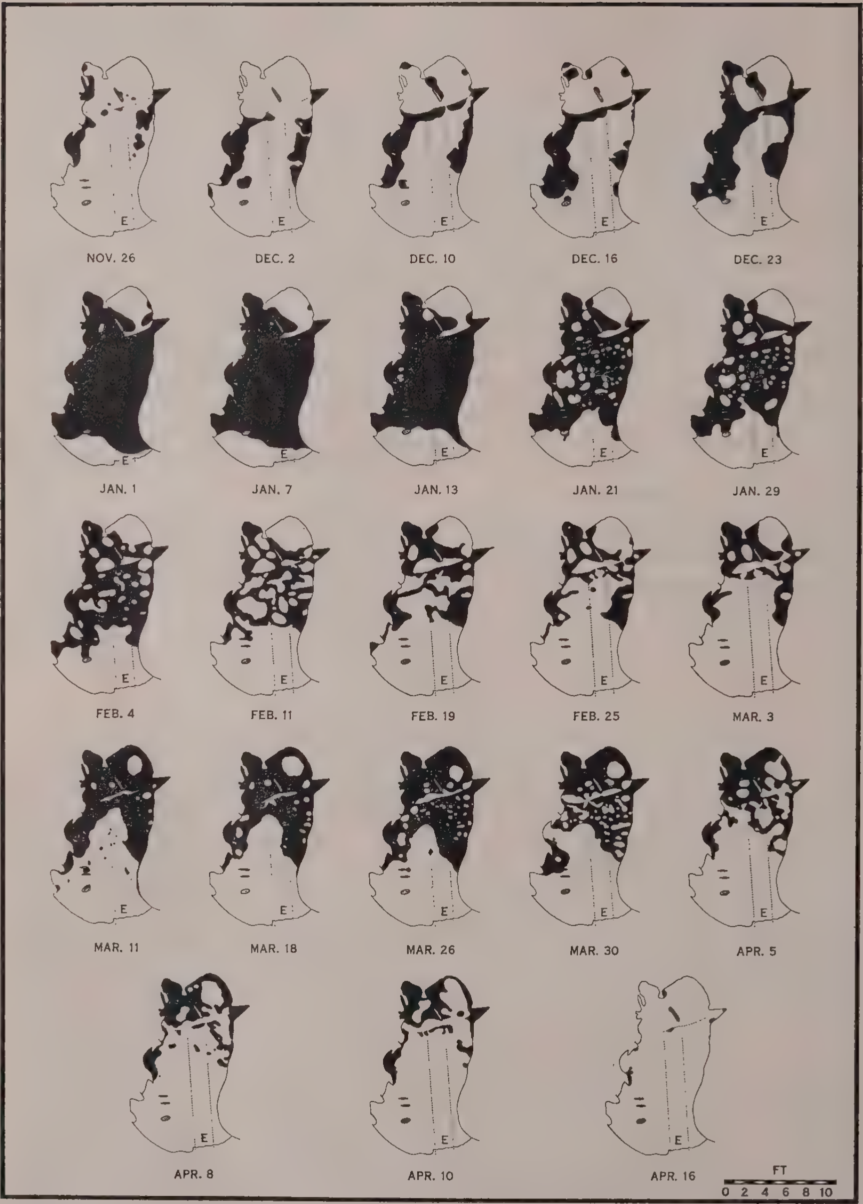


Fig. 6.—Areas covered by aestivating *A. infusa* moths on the roof of the chief observation cave at Mt. Gingera, A.C.T., during the 1952-53 season (*E*, entrance to the trench).

Both in the 1951-52 and 1952-53 seasons, a small cave containing about 10,000 moths was closed up with wire gauze from January 10 to mid April and from December 10 to mid April respectively. Although mortality was considerable, especially in the latter summer, many of the moths maintained their normal resting pattern on the roof of the cave. Only during April each year, when the autumn migrations were in progress, did they appear to become greatly agitated by their confinement, when they were soon denuded of scales and clustered in small groups on the wire gauze. It has been concluded therefore that many of the moths are able to remain in aestivation for periods of up to 4 months.

(*b*) *Activity during Aestivation*

In the summer of 1951, it was noticed that a small proportion of the moths became active shortly after sunset each evening and many of these indulged in an intense, random flight over the summit of the mountain. The flight period lasted for a little more than an hour, when the majority of the moths returned to their shelters and all activity ceased.

This unexpected behaviour was further investigated during the past two seasons. Typical of a series of these observations were those made on January 2, 1952, when the sun set at 7.25 p.m. in a clear sky. The air temperature at sunset was 13·6°C and a slight breeze was blowing from the south-west. A few moths were already crawling about and vibrating their wings 25 min before sunset, while others were flying about slowly within the cave. Their vibrating wings produced a subdued buzzing sound and any sudden sharp noise was followed by an immediate burst of activity. An occasional moth flew spasmodically over the rocks outside the caves during the next few minutes, but usually returned to the shelters within a few seconds of emergence. Ten min before sunset numerous moths were flying about just within the cave entrances and many more had crawled away from the masses and had spread out over the rocks. The numbers of moths flying over the summit had increased slightly, but within the next 5 min hundreds of moths were emerging from the caves and joining those in flight outside. The density and intensity of the flight over the outcrops increased very rapidly during the next 20 min. Their flight appeared to be completely random in character and, at its height, the noise was distinctly audible as a low, intense buzzing. The sound made by the frequent collisions of moths in flight was also audible as a constant clicking. The flight had waned considerably 60 min after sunset and many moths were observed returning to the caves. Within the next 20 min most of the moths had returned.

Observations within the flight area and around its margins during the period of activity suggested that the moths did not attempt to fly away from the mountain, nor were any observed to feed at flowers in the area. Furthermore, the flight had no mating function for copulation was not noticed despite careful observation. This was confirmed by dissecting samples of 100 females taken at random from the caves at weekly intervals throughout the summer. Without exception the ovaries were immature and no spermatophores occurred in the bursa copulatrix where they are normally deposited during copulation.

At the height of the flight the margins of the moth masses receded only an inch or two, and the great majority of the moths showed no inclination to move. Many that left the masses did not join the flight outside but either crawled around nearby, sometimes with wings vibrating, or rested on the rock surfaces. Activity was therefore represented by crawling, wing vibration, slow flight within the caves, or by the intense random flight above the outcrops. The period of activity coincided with the period of rapidly changing light intensity and it seemed probable that this was the stimulus that initiated activity behaviour.

A similar burst of activity accompanied the change of light intensity at dawn on January 3. The air temperature was 6·5°C 70 min before sunrise. Only an occasional moth was then crawling away from the masses but a very subdued buzzing sound from the depths of the caves suggested that some activity could be expected. An hour before sunrise a few moths were in flight over the summit when there was sufficient light to enable one to distinguish the outlines of the rocks. Ten min later the flight had increased in intensity and the moths were flying in the same random fashion, particularly on the lighter side of the summit. A marked flight was in progress 30 min before sunrise and many moths had spread out over the rock surfaces within the caves. It was then sufficiently light to enable notes to be made without the aid of a lamp. Presumably because of the lower temperature, the flight was not as intense as on the previous evening. The flight had begun to wane rapidly 10 min before sunrise and the moths were re-entering the caves in a steady stream. Those remaining in flight kept close to the ground or on the shaded sides of the outcrops. By the time the sun rose at 4.50 a.m., the last moths were retiring to their shelters, but the crawling and wing-vibrating activity within the caves persisted for about another 15 min.

From these and the earlier observations it was clear that the aestivating moths had two normal periods of activity each day, coinciding with the periods of rapidly changing light intensity at dusk and at dawn. Laboratory experiments showed that this is also the period of pigment migration in the eyes of *A. infusa.* Further, the pigment in the eyes of moths kept in constant darkness remained in the dark-adapted proximal position, whereas it remained in the light-adapted distal position in those kept in constant light. There is therefore no inherent diurnal rhythm of pigment migration in this species. As in many other Lepidoptera, the dark-adapted eye glowed a bright red colour when suddenly subjected to a strong light, and when the eyes were in this condition the active moths were strongly phototactic.

In later observations a technique was devised to demonstrate more precisely the trend of moth activity. As crawling always preceded flight and as activity was often expressed only as crawling, measurements were made of the number of moths engaged in this form of activity. The number of moths crawling may not, of course, bear a constant relationship to the number flying.

For this purpose 10 squares, each with a 12-in. side, were drawn with white waterproof ink on the rock surfaces towards the entrances of two of the main observation caves. The moths resting or crawling in each of these squares were counted at 4-min intervals during the evening and morning flight periods or, on one occasion, throughout the night.

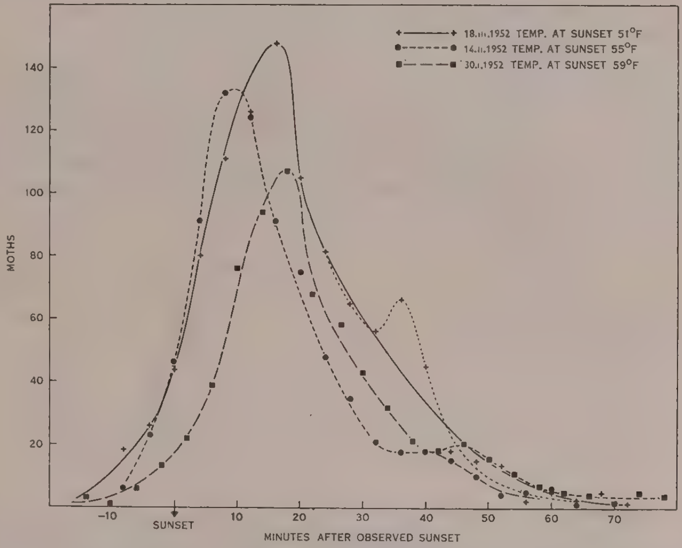


Fig. 7.—Moth activity related to time before and after observed sunset at Mt. Gingera, A.C.T. January 30, 1952: dense smoke haze with light failing gradually 80 min before sunset. February 14, 1952: sun sank behind cloud on horizon 6 min before sunset. March 18, 1952: sun obscured by cloud until 71 min before sunset and then again from 23 to 13 min before sunset.

The maximum moth activity determined by this method occurred on five evenings, with varying conditions of cloud and smoke haze, from 8 to 20 min after sunset (Figs. 5 and 7). On three of these evenings, when the light intensity was measured at one of the observation squares, the maximum activity was recorded when the light intensity had declined to 0·06 f.c. (Fig. 8). This corresponded to a light intensity of approximately 0·71 f.c. in a completely exposed position beyond the caves (Fig. 9). Early morning activity related to light intensity resulted in a curve with two peaks, the first at a light intensity of 0·07 f.c. and the second at 1·26 f.c. (Fig. 10). The light intensity was measured at short intervals with an S.E.I. photometer on a square of Bristol board used for all the measurements.

On two occasions, when dense clouds suddenly obscured the sun during the early afternoon, minor bursts of moth activity have been observed. One of these resulted in a sparse but well-defined flight over the outcrops, even while a hail storm was in progress. All activity ceased when the sun again appeared.

Although activity was reduced at temperatures below about 7°C, the number of moths crawling within the caves appeared to vary considerably from night to night even at reasonably comparable temperatures. At 2·4°C on one occasion no flight occurred and few moths left the masses during the flight period. Evening flights towards the end of the summer appeared to increase both in density and intensity, even at temperatures below 7°C.

No serious attempt has been made to measure the trend of flight activity as opposed to crawling activity, but there was probably a general agreement between the two. The peak of flight activity, of course, occurred a little later than that of crawling activity, the delay being roughly estimated to be about 10-15 min. From Figure 9 the peak of the flight would therefore also have occurred at a light intensity of approximately 0·06 f.c.

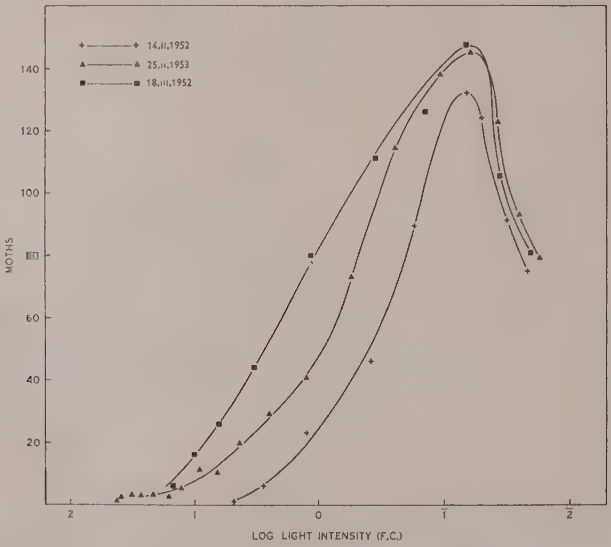


Fig. 8.—Moth activity on three evenings related to light intensity, measured with an S.E.I. photometer at one of the 10 observation squares, Mt. Gingera, A.C.T.

(*c*) *Incidence of Feeding During Aestivation*

Every effort was made to determine whether any of the moths sought food during the evening or morning flight. Only once, on January 21, 1953, a few moths were noticed feeding at flowers of *Eucalyptus niphophila* near the entrance to one of the caves. Many trees were in flower, yet less than a dozen of the thousands of moths in flight were observed feeding. During the flight period many moths settle momentarily on leaves and rocks. In those that thus settled on the flowers, the feeding response was probably initiated by physical contact with the nectar. Each of the moths remained on the one flower for several minutes and did not move actively from flower to flower as they normally do when foraging.

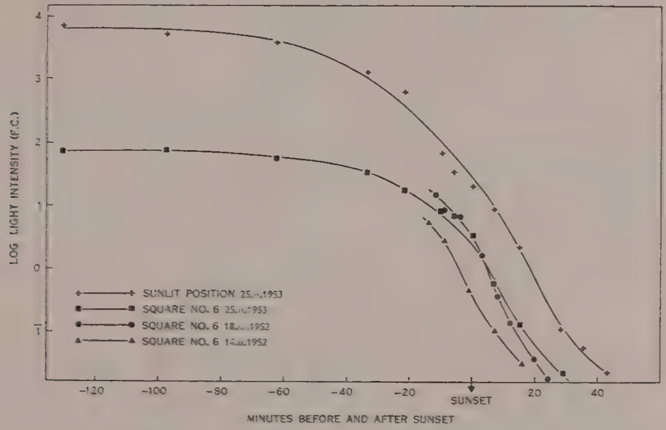


Fig. 9.—Changing light intensity at one of the 10 observation squares on three evenings and in a sunlit position beyond the caves on one evening, Mt. Gingera, A.C.T.

The following week an experiment was conducted at Mt. Gingera to determine whether the moths seek food during the evening flight. Seven groups of three petri dishes containing cotton wool saturated with three liquids were set out at the beginning of the flight period on suitable flat rocks at the summit. Each group of dishes included one of each of the following: water, 2M sucrose solution, or fermenting molasses solution (made up the previous day by mixing 4 teaspoons of molasses, 1 teaspoon of powdered yeast, and 400 ml water). At 5-min intervals throughout the flight period, the moths that settled on the dishes were counted. Thousands of moths took part in the flight above the rocks, but only 22 were counted on the dishes, all but one of which were on the sugar solution. The remaining moth was on the fermenting molasses. Many

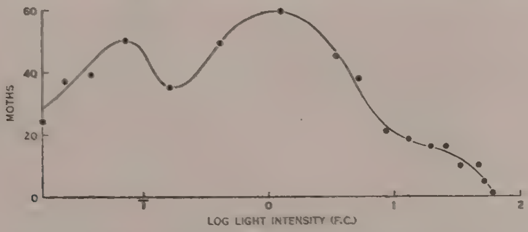


Fig. 10.—Moth activity in the early morning related to light intensity at one of the 10 observation squares, February 26, 1953, Mt. Gingera, A.C.T.

moths settled momentarily on the rock surfaces within an inch or two of the dishes, but did not crawl towards them. Moths appeared to settle on the dishes at random, but only those settling on the sugar solution remained to feed.

A second, unreplicated test was conducted on February 25 in the same situation with two 12-in. square trays. Each was covered with a layer of cotton wool, one saturated with a solution of honey and the other with water. The trays were placed about 12 in. apart and their positions were interchanged once during the experiment. Moths feeding at each tray were counted at 4-min intervals throughout the flight period. A total of only 14 moths was observed feeding and all of these were on the tray containing honey solution.

The results of these experiments suggest that moths engaged in the twilight flight normally seek neither food nor water. However, if they happen to settle on sugary food, the feeding response may be elicited.

(*d*) *Sex Ratio of Aestivating Moths*

Samples of moths varying in number from 135 to 1059 were taken from the caves, often at weekly intervals, in both the 1951-52 and 1952-53 seasons to determine the sex ratio. Only once, on April 17, 1952, were females in excess of males, when the percentage of males in the smallest sample of 135 was 45·2. Excluding this sample, the proportion of males in 1951-52 ranged from 52·7 to 66·4 per cent. with a mean of 58·5 per cent. The following year it ranged from 53·2 to 68·4 per cent. with a mean of 61·5 per cent.

Of 724 moths reared simultaneously from eggs laid by adults collected in the caves at Mt. Gingera in April 1951, 51·9 per cent. were males. Each year the proportion of males from the caves was significantly greater than that in the reared material.

Although the males of some noctuids often come to light in excess of females, males comprised 49·9 per cent. of the collections of *A. infusa* from the high-intensity light trap and 52·9 per cent. of those from the low-intensity light trap at Canberra between September and December 1952. The total catches of this species numbered 3295 and 694 respectively. As this was the period of the spring migrations, it is assumed that most of these moths were taken during migration.

There appears to be no simple explanation for the slightly higher proportion of males taken on most occasions from the assemblages of aestivating moths.

(*e*) *Parasites and Predators*

It would be surprising if such large aggregations of aestivating moths were not subjected to parasitism or predation. However, observations suggested that predation at least is not of great importance.

Bennett (1834) stated that crows (*Corvus* sp.) fed upon the moths during the summer and they in turn were used by the aborigines as food. Leithhead (1951) saw a flock of crows attacking moths in a camp at the summit of Mt. Jagungal (6758 ft) in the Snowy Mountains. Flocks of crows were not unusual in the vicinity of rock outcrops, both in the Brindabella Range and the Snowy

Mountains, even where there were no signs of moth occupation. Currawongs (*Strepera graculina* Shaw and *S. versicolor* Latham) were observed feeding on bogong moths on April 8, 1953, at the Mt. Gingera camp. The birds were perched in nearby trees and swooped down to capture moths which had been disturbed and flew from the caves. Crows or currawongs probably also enter the lighter caves and feed on the moths *in situ*, for bird excrement and fragmented moths were often noticed in these caves.

Bats were plentiful during the evening flight period, hawking above the rock outcrops, and occasionally owls were also active. On several occasions rats were noticed in the caves and were probably responsible for the death of some moths found with their abdomens removed. Specimens were not captured but it is probable they were one of the native species of *Rattus*.

In April 1952, an extremely cold change killed many of the moths that had not already migrated. Fresh fox tracks on the snow converged upon the heaps of comatose moths, which had been scratched about. Fox dung was densely packed with the chitinous remains of the moths. These insects may not usually form a part of the diet of foxes in this area; perhaps the early fall of snow provided a ready source of food in otherwise harsh circumstances.

A mermithid nematode parasite was plentiful at Mt. Gingera and many of the moths died when the mature larval nematodes emerged from their hosts in the latter half of January and early February. The nematodes then tunnelled into the moist debris on the cave floors, where they remained at depths of 9-15 in. during the winter. Mature larval nematodes collected in these situations in early October 1952 and kept in the laboratory at 4·5°C moulted to adults shortly afterwards, but neither copulation nor oviposition was observed during the next few weeks. However, eggs which were perhaps laid by adults of the previous generation were common in the debris in October and a few hatched in the laboratory.

In 1953 the first nematodes were observed emerging from dying moths on the floor of the caves on January 7 and their numbers reached a maximum about January 29. Only a few freshly emerged worms were noticed on February 11 and thereafter none were seen. At this time they were numerous about 2 in. beneath the surface of the floor debris and, during the next few weeks, gradually worked their way deeper. The pH of the surface debris on January 29 was 3·9 and at a depth of about 8 in. was 4·1.

As none of the nematodes has been dissected from moths taken anywhere but in the camps which appear to be occupied each year and, as the larval nematodes pass the winter in the debris on the floor of the caves, it has been concluded that the life cycle of this parasite has been nicely adapted to the aestivation habit of its host. Mermithids usually parasitize the larvae of their insect hosts and this is probably the first record of an adult lepidopteron being parasitized by these nematodes.

(*f*) *Fat Content of Moths at Mt. Gingera*

Dissections of moths taken from Mt. Gingera throughout the 1951-52 season, as well as those collected in light traps at Canberra during the spring migrations, showed that their fat reserves were generally high and the ovaries of the females immature.

Beall (1948) estimated the fat content of samples of the butterfly *Danaus plexippus* Linn., taken at various localities in North America during its migratory cycle. He found that butterflies from overwintering clusters in California had a fat content of about 30 per cent. of their dry weight, although those taken in Louisiana in the autumn, apparently after a long migration from the north, had practically exhausted their fat reserves. It is probable, therefore, that *D. plexippus* is able to recuperate its fat loss in its wintering place, apparently just before or during hibernation.

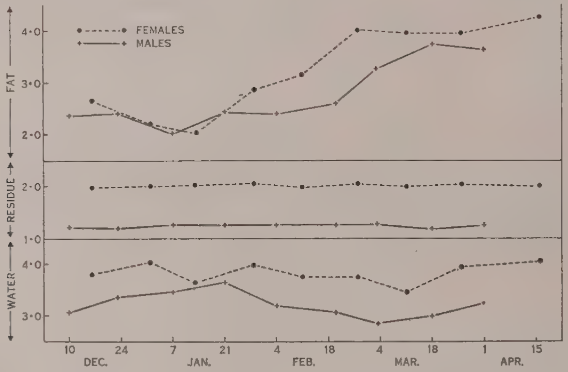


Fig. 11.—Mean weight (g) of fat, dry fat-free residue, and water in the abdomens of samples of 60 male and female *A. infusa* moths taken at fortnightly intervals during 1952-53 season, Mt. Gingera, A.C.T.

Estimations of the fat content of *A. infusa* taken in the Mt. Gingera camp were made between December 10, 1952 and April 16, 1953. Both Beall (1948) and Williams (1945) found that the percentage of fat in migrating Lepidoptera varied greatly from one individual to another, depending apparently on various factors, including the distance the insects had migrated. In anticipation of such individual variation, samples of 360 bogong moths of each sex were used for the estimations. Each sample was divided into six equal replicates and the fat content of males and females was estimated on alternate weeks. Altogether, nine estimations were made at fortnightly intervals on each sex. Only the abdomens of *A. infusa* were used, since Williams (1945) had shown that a large proportion of the fat reserves of the migratory moth, *Plusia gamma* (Linn.), was contained in the abdomen.

The abdomens were removed after anaesthetization with carbon dioxide, weighed, and dried over phosphorus pentoxide. The fat was then extracted with ether in a Soxhlet apparatus for about 15 hr and the fat-free residue was again weighed.

The fat content of the moth abdomens (Table 3) showed a significant upward trend after the middle of January. Although this suggests that the moths fed during aestivation, there is strong circumstantial evidence against this. It is more likely, therefore, that increases in the average fat content were correlated with the changes in the population described earlier.

TABLE 3

ANALYSES OF THE ABDOMENS OF *A. INFUSA* ADULTS DURING 1952-53 SEASON AT MT. GINGERA

Date	Mean Weight (g)						Percentage Fat	
	Male			Female				
	Water	Lean Wt.	Fat	Water	Lean Wt.	Fat	♂	♀
10.xii.1952	3·0619	1·2011	2·3495				66·2	
18.xii.1952				3·8008	1·9878	2·6502		57·1
24.xii.1952	3·3665	1·1948	2·4143				66·9	
2.i.1953				4·0432	1·9576	2·2920		53·9
7.i.1953	3·4718	1·2600	2·0280				61·7	
14.i.1953				3·6217	2·0144	2·0507		51·6
23.i.1953	3·6410	1·2582	2·4156				65·8	
30.i.1953				4·0061	2·0862	2·8710		57·9
5.ii.1953	3·1923	1·2798	2·4078				65·3	
12.ii.1953				3·7598	1·9984	3·1499		61·2
20.ii.1953	3·0886	1·2715	2·6039				67·2	
27.ii.1953				3·7785	2·0300	4·0186		66·5
4.iii.1953	2·8497	1·2565	3·2861				72·3	
12.iii.1953				3·4762	1·9673	3·9597		66·8
19.iii.1953	3·0092	1·1819	3·7353				76·0	
27.iii.1953				3·9300	2·0424	3·9697		66·0
2.iv.1953	3·2476	1·2270	3·6209				74·7	
16.iv.1953				4·0367	1·9913	4·2675		68·2
16.iv.1953 (caged cave)	2·9769	1·1634	2·3196	3·7007	1·8993	2·9103	66·6	60·5
Min. diff. for signif.								
5% level	0·1156	0·0361	0·2637	0·1956	0·0914	0·4155		
1% level	0·1542	0·0481	0·3516	0·2608	0·1219	0·5540		

Fat decreased in both sexes between mid December and mid January (Fig. 11), a period of rapid population increase followed by a slight decrease (Fig. 4). Although the decrease in fat was probably due partly to metabolism, it was possibly also correlated with the population change.

The remainder of the aestivation period can be conveniently divided into four. First there was a period of steady population decline between January 13 and February 4, when there was a considerable mortality. The moths were apparently eliminated in a random manner, because small bare spaces suddenly appeared throughout the moth masses. The significant increase in the fat content of the samples at this time suggests that there had been a differential elimination of moths with depleted fat reserves.

The second period of population decline was between February 4 and February 25, when the random elimination of moths throughout the masses was accelerated. Most of this decrease was apparently due to migration. If migration was initiated by fat depletion the average increase in fat at this time could have been due to the departure of those with the lowest fat content.

During the third period, between March 3 and 26, large increases in the population occurred. This was apparently due to the arrival of moths which had already begun their migration from camps farther south. There was also a simultaneous steady movement of moths away from the mountain. During the autumn migration moths probably again feed freely, for laboratory experiments have shown that it is a necessary prerequisite to copulation and oviposition in the aestivating moths. This may account for the maintenance of the high fat content of the female samples and the further significant increase in that of the males.

Finally, after March 26 there was a rapid decrease in the moth population at Mt. Gingera, when there was no significant fluctuation in the average fat content in either sex. Again it may have been maintained by the steady arrival of migrants that had been feeding *en route*.

Unfortunately it was not possible to make simultaneous fat estimations on the moths in the caged cave. However, an estimation was done on a sample of 360 males and 294 females taken from this cave on April 17, when most of the uncaged moth population had migrated. Their fat content did not differ significantly from that on December 10, when the cave was closed up. On the other hand, it was significantly lower than the April estimations on the uncaged population. There was a considerable mortality in this cave during the second half of January and February. Some of this was clearly due to parasitism, but it is probable that many of the moths that would have migrated died. The average fat content of moths in this cave probably also fluctuated but, as there was no influx of moths in March, the average fat content may have gradually decreased to its final figure.

The dry fat-free ("lean") weight of the moth samples showed only slight seasonal variation compared with the weight of fat. In males it showed a more decided trend than in females. There was a significant rise between December 24 and January 7, after which it remained more or less constant until early March, when there was a significant decrease followed by another significant increase on April 2. These changes occurred when gross changes in the composition of the moth population were recorded (Fig. 4).

As the moths probably ingest moisture during aestivation, it is not surprising that the water content of the moth samples varied greatly. The lowest water content was recorded early in March, after a dry period of several weeks. During this dry period, the moths produced little excrement when disturbed, but after rain it was much more copious. Their water excretion and hence their water content depended upon moisture availability.

VIII. ORIGIN OF THE MOTH POPULATIONS

One of the earliest reports of economic damage by the larvae of *A. infusa* was by Olliff (1890) who referred to it as a pest of maize in New South Wales. An extensive outbreak throughout the Tablelands and Western Slopes of New South Wales was described by Froggatt (1900). Large areas of winter wheat crops and pastures were injured by the larvae, which attacked on a front, destroying everything before them. In undulating country the damage was more severe on the black soil flats. Adults emerged from these larvae in October. Further damage was recorded in the Narrandera area (Anon. 1901) and at Whitton, Condobolin, and Trundle the following year (Froggatt 1902).

Larvae were again noticed by Froggatt (1907) on alluvial flats in the Tamworth district in August 1906, but widespread damage was not reported again until 1909 when saltbush was severely attacked at Hay during the winter and spring (Froggatt 1910). Wheat crops in the Ganmain, Yanco, Narrandera, and Grong Grong districts suffered injury again in September 1911 (Froggatt 1911).

There are few other specific references to damage by *A. infusa*. In Queensland, cutworm injury to cabbages was referred to two species, *A. spina* and *A. radians* (Anon. 1925). The former species was also reported to be injurious to young grape vines in the Murray Valley (Lyon 1925). In Western Australia, Newman (1927) stated that *A. infusa* larvae were numerous in some seasons. Since the reports by Froggatt, the Australian economic literature contains many references to injurious attacks by cutworms without referring to any species specifically.

Field surveys were made by the author in 1952 over a wide area of the Tablelands, Western Slopes, and Western Plains of New South Wales. Larvae were not discovered during the summer in the vicinity of the aestivation camps, despite careful search. They were found to be extremely numerous, however, in winter pastures, particularly in northern New South Wales, but were also common in many other parts of the State (Fig. 1). The densest larval populations were found on heavy self-muching soils on the North West Plains and North West Slopes. Much damage due to *A. infusa* was observed in linseed crops in the Yetman district (Plate 3, Fig. 2), and similar damage was caused to linseed at Milmerran on the Darling Downs (J. Macqueen, personal communication). In pastures on heavy soils, larvae were most abundant in dense stands of *Medicago* spp. (Plate 3, Fig. 1). They were not found at all on the lighter soils where crowfoot (*Erodium cygnorum* Nees) or barley grass (***Hordeum leporinum*** Link.) were dominant.

In southern New South Wales, the larvae were most common on the saltbush plains south of Hay, in stands of *Medicago* spp. on self-mulching soils in slightly depressed areas. They were also numerous amongst annual composites in a degenerate pasture on a heavy brown soil near Berrigan, in a sown pasture containing clover and cape-weed (*Cryptostemma calendula* (L.) Druce) on an alluvial river flat at Corowa, and in stands of cape-weed in sown pastures on the Southern Tablelands and South Western Slopes. They also occurred, in smaller numbers, in subterranean clover pastures, in lucerne fields, and in a mixed pasture of clover and oats.

The climate of the North West and South West Wheat Belts of New South Wales, two of the areas in which the larvae of *A. infusa* occurred in greatest numbers, was described by Hounam (1947, 1950). The average annual rainfall in the north decreases from over 30 in. in the eastern section of the Northern Tablelands to less than 18 in. west of the Barwon River. Average monthly rainfall figures show that there is a preponderance of rain in the summer, but effective rains also occur in the winter. The late winter and early spring months show the least rainfall.

The average annual rainfall in the southern area ranges from over 22 in. on the Western Slopes to less than 14 in. west of Deniliquin. Here the average monthly rainfall shows a fairly even distribution, with a maximum in June. Over a wide area there is a secondary maximum in either December or January.

In both areas summer temperatures are high, and severe frosts occur in the winter.

In 1952 the larvae of *A. infusa* appeared to be largely confined to the heavy soils, and Froggatt (1900) also noticed that the most severe damage occurred on black soil flats. Heavy soils of various types supporting characteristic plant communities (see Beadle 1948) occur over extensive areas of New South Wales west of the Tablelands, and can be regarded as potentially favourable breeding areas for *A. infusa* (Fig. 1). In addition there are innumerable localized areas of heavy soils, particularly along rivers and creeks.

Medicago spp., which figure prominently in the herbaceous stratum of most of these communities during the winter (Beadle 1948; Clark 1948; Biddiscombe 1953; Moore 1953) appeared to be the most important hosts of *A. infusa*. Other pasture species probably contribute in areas where *Medicago* is not of great importance or in seasons unfavourable to *Medicago*. These include cape-weed (*Cryptostemma calendula*) and possibly some of the saltbushes which were attacked in the Hay district in 1909 (Froggatt 1910). The introduced *Medicago* spp. now form such an important element in the winter pastures that it is difficult to determine what were the dominant winter species that provided larval food for the large populations of *A. infusa* before European settlement. Laboratory experience supports field observations, however, that grasses are usually avoided by the larvae.

Data accompanying specimens of larvae of *A. infusa* in the collection of the New South Wales Department of Agriculture show that wheat, cabbages, cauliflowers, silver beet, peas, potatoes, and lucerne are also attacked. All these records of economic damage were in late winter and early spring. Some are from districts on the north and central coast of New South Wales. Only occasional larvae have been found during the summer, in gardens at Canberra.

Winter surveys in 1952 on the Southern Tableland showed that larvae had reached about the third instar in June. Thereafter slow growth was maintained and larvae in the final instar were collected mostly in late August and early September. However, some of the larvae had apparently developed more slowly, for half-grown larvae were not uncommon in northern New South Wales in September along with mature larvae. Larvae taken from linseed crops were invariably mature and pupated in the laboratory at the end of September.

These surveys have shown, therefore, that eggs are laid by *A. infusa* adults in the autumn over a wide area of New South Wales and even as far north as the Darling Downs in southern Queensland. The distribution of larvae in Victoria is as yet obscure, but it is probable they occur commonly in the winter, at least in the northern parts of the State. The larvae, however, appeared to be sufficiently numerous in New South Wales in 1952 to account for the immense populations of moths which took part in the spring migrations.

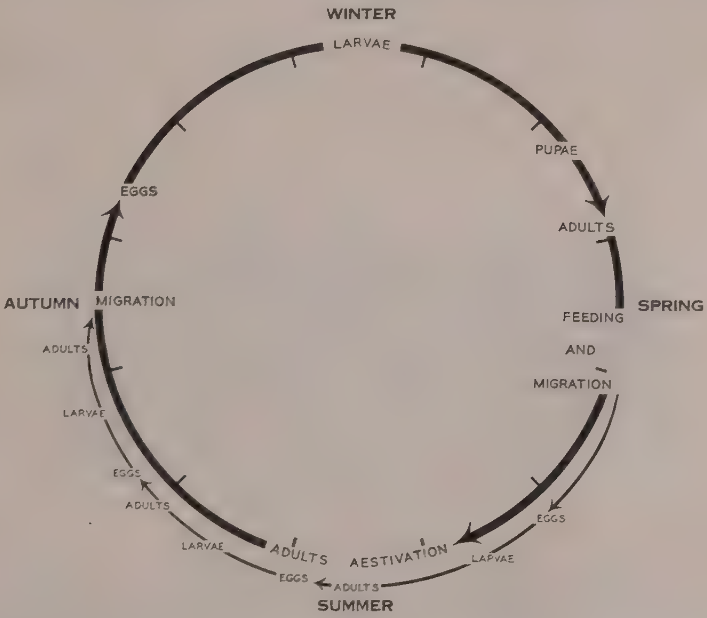


Fig. 12.—Diagrammatic representation of probable life cycle of *A. infusa.*

IX. Probable Function of Migration and Aestivation in A. infusa

There is strong evidence that large populations of the larvae of *A. infusa* occur commonly during the winter over a wide area of New South Wales. All the reported outbreaks of economic importance have occurred in the late winter and early spring, while records of the adults invading the coastal areas near Sydney and of dead moths being washed up along the coastlines of New South Wales and Victoria have been in the spring. Major migrations have also been observed in a southerly direction in the spring and early summer towards the mountains of southern New South Wales and Victoria, and a similar movement in a northerly and westerly direction away from the mountains has been observed in the late summer and early autumn. There is also evidence that very large populations of the moths aestivate in a sexually immature condition at high altitudes for a period of several weeks when they do not seek food. It has been concluded therefore that the major part of the population of *A. infusa* in south-eastern Australia has but a single generation each year. In very favourable habitats, however, three or four generations annually are theoretically possible (Fig. 12).

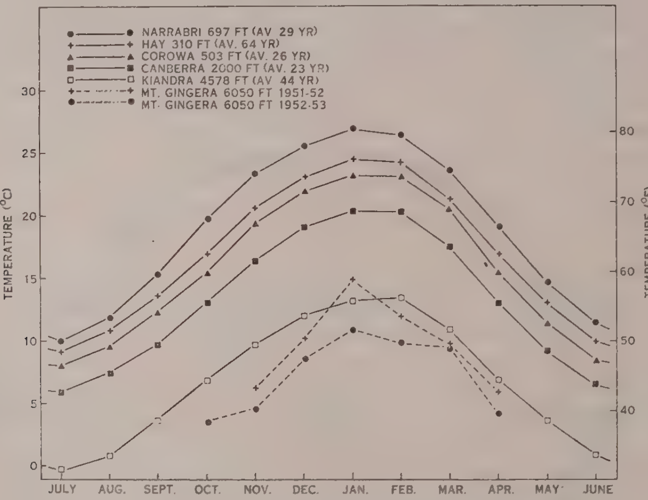


Fig. 13.—Mean monthly temperatures at Narrabri, Hay, and Corowa, compared with Canberra, A.C.T., and Kiandra (4578 ft), and within the observation caves during the 1951-52 and 1952-53 seasons at Mt. Gingera, A.C.T.

In the laboratory, eggs hatched in from 4 to 5 days at a temperature of 24°C and in about 7 days at 18°C. At 4·5°C they did not hatch at all and, when kept at this temperature for more than 4 wk, failed to hatch after they were transferred to higher temperatures. The time required for development from egg to adult at 24°C was about 7 wk and this was increased to 11 wk when the larvae were first kept for 2 wk at a temperature of 24°C, then for 4 wk at 4·5°C, and finally at 18°C until emergence. Some feeding occurred even at the lowest temperature and the rate of feeding and growth was increased immediately the larvae were returned to a higher temperature. Although larval development is delayed at a temperature of 4·5°C, no larval diapause occurs.

At a temperature of 24°C, several successive generations have been reared in the laboratory. The pre-oviposition period of adults reared at this temperature was about 7 days when fed a 2M sucrose solution and kept at a constant temperature of 15·5°C. Moths provided only with water or that were unfed did not copulate and laid but a few infertile eggs.

In contrast to this, the pre-oviposition period of spring generation moths ranged from 24 to 66 days. These data were obtained from samples of moths reared in October from mature larvae collected in northern New South Wales in late August, and from samples collected in October both at Canberra and from the gregarious assemblages near Mt. Gingera. The moths were fed in the laboratory on a 2M sucrose solution, and were kept at temperatures of 15·5-20°C. Fertile eggs were not produced at all unless the adults were provided with sugary food.

From these preliminary data it appears that a facultative diapause occurs in most of the adults of the spring generation. At the lower temperatures experienced in the mountains (Fig. 13) after migration, the time required for sexual maturation is presumably prolonged. The food ingested during the spring migration is apparently utilized to replace the fat reserves used as energy and not for sexual maturation. After aestivation, therefore, further feeding is necessary before normal mating and oviposition can ensue.

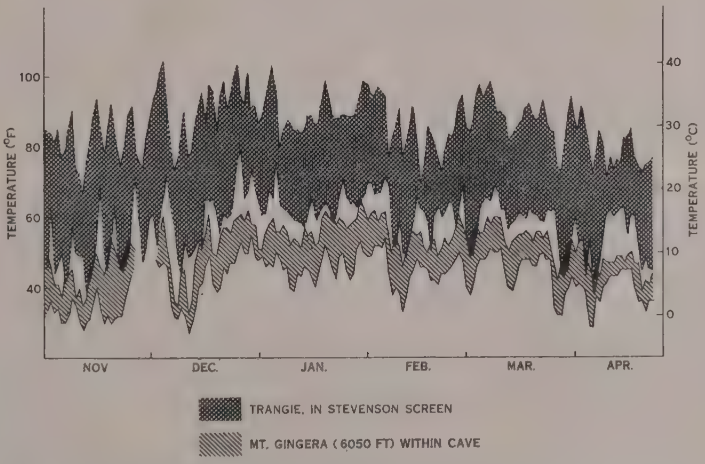


Fig. 14.—Daily maximum and minimum temperatures recorded in the chief observation cave, Mt. Gingera, A.C.T., compared with those recorded in a Stevenson screen at Trangie, N.S.W., during the 1952-53 season.

Diapause in insects is generally considered to be an adaptation which enables the species to survive in reasonably large numbers when unfavourable conditions prevail in its normal environment. In the breeding grounds of *A. infusa* perennial grasses form the bulk of the herbaceous layer during the summer, whereas the annual dicotyledons upon which the larvae feed usually flourish during the winter. At summer temperatures (Fig. 13), several generations of *A. infusa* could be completed each year if suitable food plants were available. Larval food is therefore a limiting factor during the summer and it is improbable that the species could maintain anything but a precarious existence in the perennial grass pastures at this time of the year. A diapause has probably thus arisen in the adults as an adaptation to this unfavourable summer environment.

Most insects that have developed a diapause as a response to harsh summer conditions aestivate in their breeding grounds. On the other hand, Wiltshire (1946) considered that migratory Lepidoptera do not have a diapause, assuming apparently that migration replaces diapause as an adaptation to a seasonal, unfavourable environment, enabling the insects to avoid the unfavourable conditions. If a facultative diapause does in fact occur in the adults of *A. infusa* which emerge in the spring, it is of relatively short duration and would not in itself enable the species to maintain a high population in the breeding areas. Migration, on the other hand, would appear to be an adaptation of sufficient survival value to replace diapause. However, the mean temperatures for January and February in the aestivation caves at Mt. Gingera (Fig. 14) exceeded 9·8°C during the past two summers. At a temperature of 4·5°C in the laboratory, moths reared at 24°C began to lay fertile eggs in 50 days when provided with sugary food, and at 15·5°C similar moths oviposited in 7 days. Sexual development in non-diapausing moths would apparently require much less than 50 days from metamorphosis at the temperatures operating in the aestivation shelters. It is doubtful therefore if migration without an accompanying diapause would enable moths emerging in the spring to lay their eggs after their larval food plants germinate in the autumn.

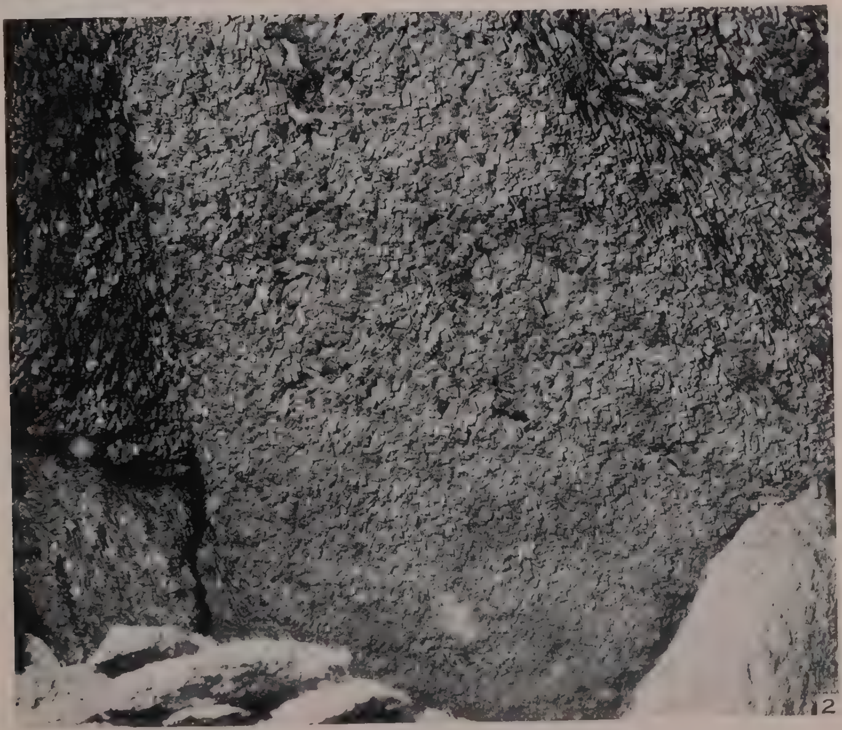
Although it is considered that the majority of the population of *A. infusa* has a single generation each year and that migration, probably accompanied by a diapause, may be essential to the survival of the species in relatively high numbers, it is probable that a small proportion of the spring generation moths do reach maturity without aestivating. A few moths that had already copulated were taken in light traps at Canberra in the spring. Localized small favourable habitats exist in irrigated areas and gardens, where suitable food plants would be available to the larvae. For example, an occasional larva has been collected in a garden at Canberra in December. However, the lack of reports of economic damage at this period of the year supports the conclusion that larvae are uncommon during the summer.

As the adults which have completed their aestivation in the mountains apparently begin to migrate back to their breeding grounds as early as the beginning of February, at least in some years, it is possible that the larvae from eggs laid by these individuals do not reach maturity. However, larval survival depends on the timely occurrence of rains to germinate their food plants and even those resulting from moths that migrate later in the summer or autumn may be greatly reduced in numbers in unfavourable years.

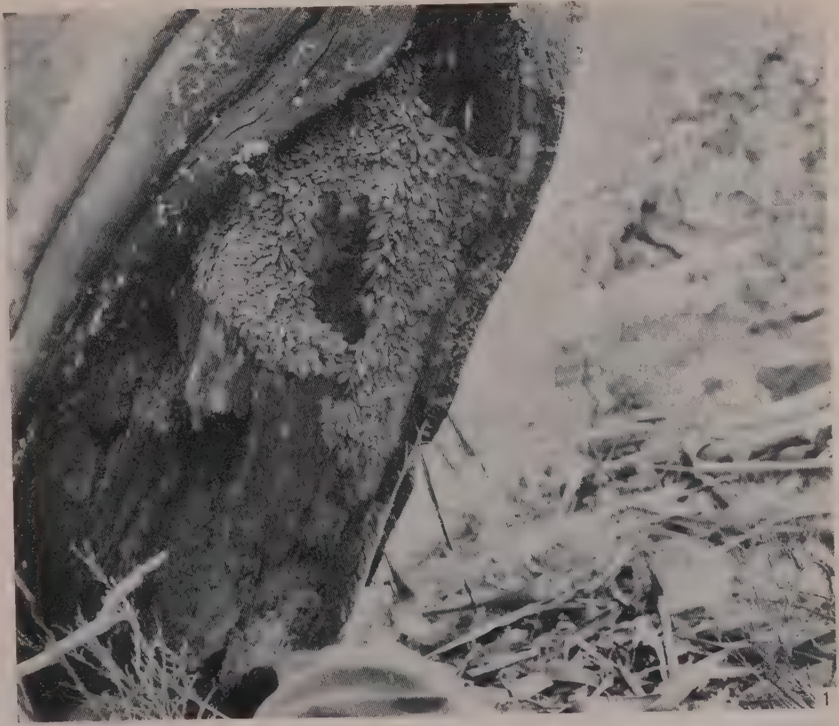
X. Discussion

In recent years the attention of various workers interested in migration has been focused on the question of a two-way migration in insects, particularly in Lepidoptera. Williams (1951) and others in Great Britain have collected much data to suggest that in several palearctic butterflies there is a conspicuous

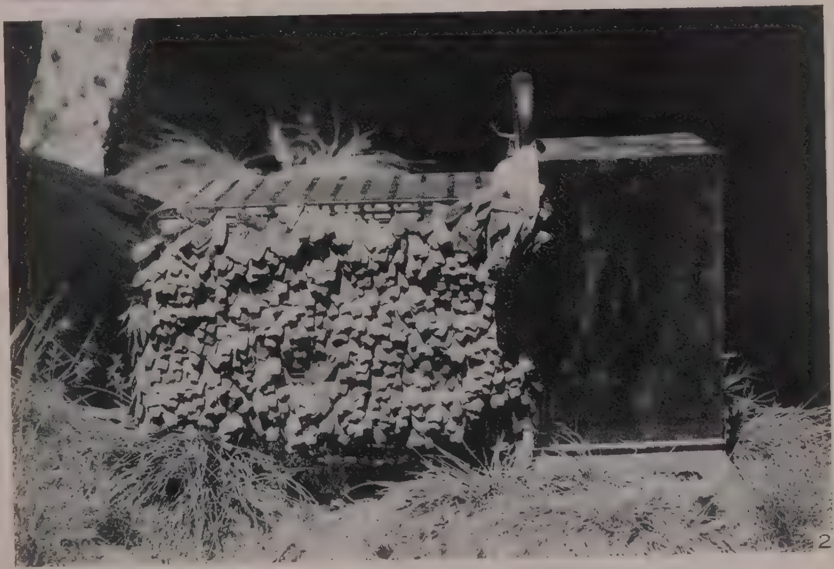
1



2



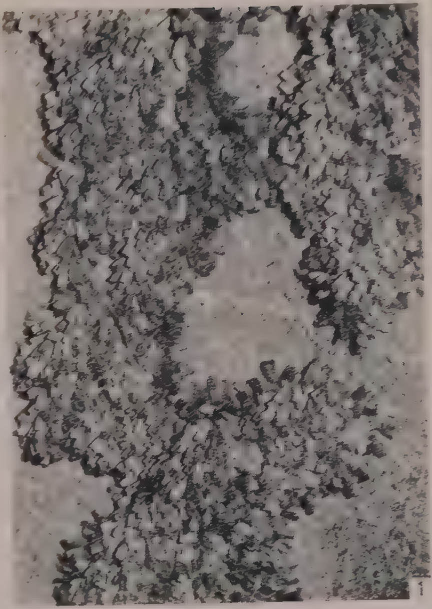
1

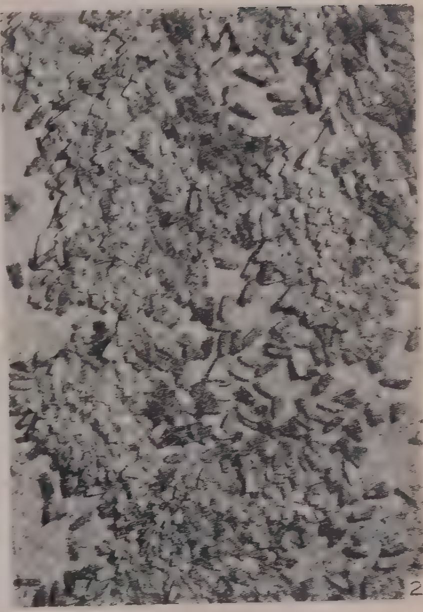


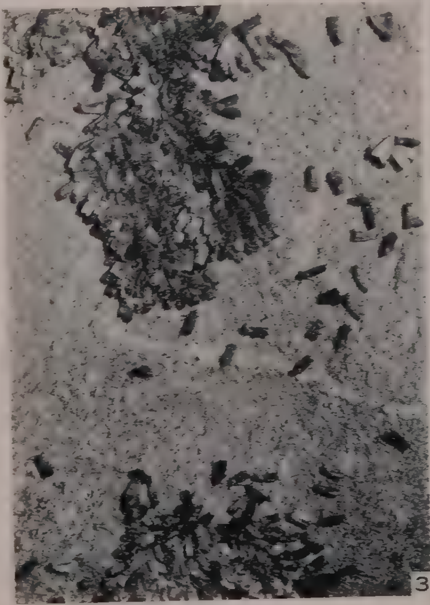
2

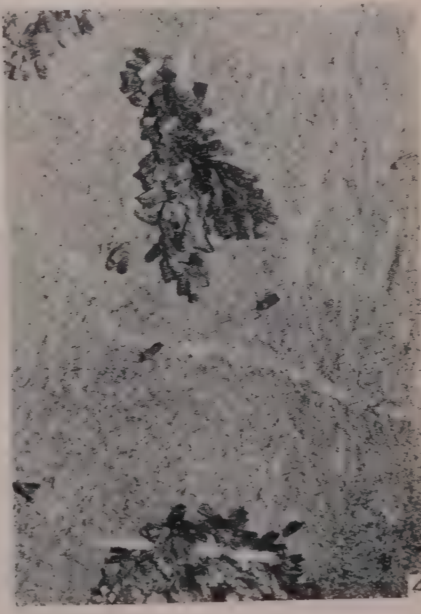
1

2


1


2


3


4

migration to the north in the spring and a much more diffuse migration in the opposite direction in the autumn. The observations of D. and E. Lack (1951) and Snow and Ross (1952) on insect migrations southward through passes in the Pyrenees in the autumn have created fresh interest. The present observations on *A. infusa* provide an example of the probable biological value of a two-way migration in the ecology of a moth.

In most migratory Lepidoptera in which a two-way migration is believed to occur, breeding apparently takes place at both ends of the migration. Thus in spring, the adults of one generation of *Vanessa cardui* Linn. migrate from North Africa to Europe, where they breed, and the adults of the resulting generation then return south in the autumn to breed again during the winter in Africa (Williams 1951). Apart from *A. infusa,* the only other lepidopteron in which the same individuals are known to engage in migration in opposite directions at different seasons is the North American monarch butterfly, *Danaus plexippus* Linn. (Williams *et al.* 1942). In the autumn these butterflies migrate south in dense swarms from Canada and northern United States to Florida, southern California, and probably Mexico, where many of them hibernate gregariously in certain trees, particularly near the coast. The following spring, the same individuals engage in a northerly, more diffuse migration, when breeding takes place. From recent evidence, Beall (1952) has suggested that many migrating *D. plexippus* do not join the hibernating clusters or, if they do, only for a relatively short time. Observations in Florida on the direction of flight of these butterflies during the winter showed that, at this latitude, the southerly migration was still in progress in December and that migration to the north had begun by early March.

Observations on *A. infusa* in the 1951-52 season (Common 1952), in which migrations were noticed only in November and April, suggested that major movements were confined to the spring and autumn. However, in the 1952-53 season a northerly movement of small magnitude had apparently begun by early February, culminating in much more spectacular migrations in early April.

The Mt. Gingera camp is one of the most northerly of the known aestivation sites and is probably used also as a temporary camp by moths which migrate farther south. Nothing is known of the behaviour of the moths in camps in the Victorian mountains. A few areas in north-eastern New South Wales would appear to be high enough to enable moths to aestivate (Fig. 1), but no summer assemblages have been reported from these mountains. If they were at all important for aestivation it seems certain they would have been known by the aborigines of the area.

Another noctuid, *Chorizagrotis auxularis* (Grote), which is a winter pest with an annual life cycle in North America, may behave in a similar manner. The large populations of moths which emerge in the spring suddenly disappear and it has been suggested by Pepper (1932) that they may migrate to the western mountains where aestivation may be possible at lower temperatures. To support this explanation, Pepper described a south-westerly unidirectional flight which he observed during the summer in Montana. Other observers since have noticed that this species is sometimes very common in the summer at altitudes of 6000-12,000 ft in the Rocky Mountains (Walkden 1950). In Egypt and in the Tal lands of India, *Agrotis ypsilon* (Hfn.), a species closely related to *A. infusa*, is also an important winter pest. Again the moths are very plentiful for only a short time in the spring. To account for their sudden disappearance, and their absence from the infested areas during the summer, Fletcher (1925) and Williams (1930) suggested that they may migrate to cooler areas, and specimens have in fact been taken on a ship in the Mediterranean Sea, along with other migrant Lepidoptera (Williams 1930). However, *A. ypsilon* normally has two or more destructive winter generations in these areas and Fletcher also stated that it breeds in the hills of India during the summer.

Williams (1949) discussed the factors that may be involved in the orientation of Lepidoptera during migration, stating that much further evidence is needed before definite conclusions can be reached. The major spring migrations of *A. infusa*, though predominantly southerly in direction, have ranged from south-east to west-south-west and usually occurred when westerly winds were blowing. However, large-scale migrations in the Australian Capital Territory on October 29 occurred in calm weather, when the sky was heavily overcast and light rain was falling. The winds have also been from the west during the autumn migration. However, the moths on one occasion continued to fly steadily northwards despite a counter wind from the east caused by the topography of the area, when the wind in more exposed situations was blowing strongly from the west. Again moths leaving the Mt. Gingera camp on April 10, 1953, flew into a light northerly wind. Whereas wind appears to be an important factor in the orientation of migratory locusts (Kennedy 1951), the present information concerning its effect on the orientation of migrating nocturnal Lepidoptera is inadequate.

When the known breeding grounds of *A. infusa* are considered in relation to the south-eastern highlands of Australia, where aestivation takes place (Fig. 1), it will be seen that many of the moths would find their way to the mountains if their displacement were in a southerly to south-easterly direction. McKeown (1935) may have been correct in suggesting that the occurrence of strong westerly winds could account for the sudden spasmodic invasions of the coastal areas near Sydney by *A. infusa* moths. However, the species is also known to breed in coastal districts and, in exceptional years, the larval populations in these areas may be high enough to account for their sudden appearance in the Sydney district, perhaps during their spring migration to the south. This may also account for their movements out to sea.

As all the late summer and autumn migrations of *A. infusa* have been noticed within 1 mile of the Mt. Gingera camp, despite a careful watch farther away, the autumn movement would appear to be more in the nature of a dispersal. The observed directions of flight have ranged from north-west to west and support the conclusion that the migrating moths were then returning to their breeding grounds. Further, the autumn migrations have not been reflected in the light trap catches at Canberra (Fig. 3).

The average fat content of aestivating moths was found to be high throughout the summer, a result supported by the reported habits of the aborigines who fed on the moths mainly in January and February although they sometimes collected them as early as October (Helms 1890). Beall's (1948) estimation of the fat content of hibernating *Danaus plexippus* in California showed that its fat reserves were about 30 per cent. of its dry weight, compared with about 65 per cent. in *A. infusa*. It is not surprising perhaps that *D. plexippus* often feeds at flowers in the vicinity of the hibernating clusters on sunny days. The need for the majority of *A. infusa* to feed during aestivation would appear to be slight. Williams (1945) found that the fat contents of two migrant moths, *Plusia gamma* and *Phlogophora meticulosa* (Linn.), taken on the south coast of England in August, were about 45 and 20 per cent. respectively. In all these estimations it was found that the material used was extremely variable. For example, in *A. infusa* the average standard deviation exceeded the mean fat content, which suggests a highly skew distribution. The heterogeneity of the fat content is probably correlated with the heterogeneous origin of the moths, both with regard to the distance migrated and the climate of the larval environment.

The apparent absence of feeding and mating is not the only unusual feature of the behaviour of the aestivating adults of *A. infusa*. The close correlation between the period of activity and the period of changing light intensity after sunset and before sunrise has probably not been demonstrated previously in any noctuid. Most noctuids certainly become active during the period of rapidly changing light intensity in the evening, but normally their activity is maintained for some of the remaining hours of darkness. The spring migrations of *A. infusa* were continued late into the evening and, on February 25, 1953, migrating moths continued to arrive at the summit of Mt. Gingera from the south throughout the night (Fig. 5). Larsen (1949) found that migratory flight activity in *Plusia gamma*, a species that is also active in the daytime, continued until after midnight, whereas feeding activity occurred about midday and again at the change from light to darkness. The day time activity was temperature-dependent, while in the evening it appeared to be mainly dependent on light. On the other hand, Collins (1934) found that the codling moth (*Carpocapsa pomonella* Linn.) is usually active only during the periods of changing light intensity, when feeding and reproduction occur. As in *A. infusa* and other species, this was also the period of pigment migration in the eyes of *C. pomonella*.

It is probable that the large aestivating populations of *A. infusa* usually originate in extensive tracts of heavy soils on the Western Slopes and Plains of New South Wales. The winter is passed in the larval state, when feeding apparently continues at a slow rate if the temperature is high enough. In contrast to this, one of the other important cutworms in eastern Australia (*Euxoa radians* Guen.) survives the winter as a pupa in areas where frosts occur. Furthermore, crop damage by the larvae of *E. radians* occurs mainly on the lighter soils (Currie 1930). Cutworm outbreaks during the winter and early spring in the wheatgrowing areas of New South Wales and southern Queensland cannot therefore be due to the latter species.

The field observations, supplemented by preliminary laboratory experiments, suggest that a facultative diapause occurs in the adults of the spring generation of *A. infusa*. The induction of diapause in the pupa of *Diataraxia oleracea* Linn. (Way and Hopkins 1950) and in the larva of *Grapholitha molesta* (Busck) (Dickson 1949), was influenced by the photoperiod and temperatures operating during larval development. Whatever the cause, it seems that a diapause in *A. infusa* has probably arisen as an adaptation to the unfavourable summer conditions characteristic of the breeding grounds. The dicotyledonous larval food plants are usually abundant in the winter, but are normally replaced by unpalatable perennial grasses in the summer. Furthermore, the ability to migrate for the summer to an environment more favourable to the adults has also developed. Long distance migration may not be possible in this species unless an adult diapause has been induced, because at the temperatures prevailing in the breeding grounds during the spring, sexual maturation would be rapid if the moths fed freely, as they do during migration. Adult diapause may in fact be characteristic of some multivoltine Lepidoptera that migrate long distances. It would be interesting for example to know whether an adult diapause occurs in the autumn generation of *Danaus plexippus*.

XI. Acknowledgments

The author is grateful to many colleagues in the Division of Entomology for helpful discussions and other assistance; to Mr. G. A. McIntyre for the statistical analyses, to Mr. C. H. Williams, of the Division of Plant Industry, for the pH determinations; to Mr. L. A. Marshall and Mrs. B. Perry, who drew the figures; and to Mr. D. Wilson for photographic advice. Special thanks are due to Mr. R. F. Powning, who undertook the fat estimations, and to Dr. R. Carrick, of the Wildlife Survey Section, C.S.I.R.O., for the excellent flashlight photographs in Plate 4.

XII. References

Anon. (1901).—The caterpillar plague. *Agric. Gaz. N.S.W.* **11**: 657.

Anon. (1925).—Cutworms and cabbages. *Qd. Agric. J.* **23**: 523-4.

Beadle, N. C. W. (1948).—"The Vegetation and Pastures of Western New South Wales with Special Reference to Soil Erosion." 281 pp. (Govt. Printer: Sydney.)

Beall, G. (1948).—The fat content of a butterfly, *Danaus plexippus* Linn., as affected by migration. *Ecology* **29**: 80-94.

Beall, G. (1952).—Migration of the monarch butterfly during the winter. *Lepid. News* **6**: 69-70.

Bennett, G. (1834).—"Wanderings in New South Wales, Batavia, Pedir Coast, Singapore and China." 2 Vols., 440 and 428 pp. (Richard Bentley: London.)

Biddiscombe, E. F. (1953).—A survey of the natural pastures of the Trangie district, New South Wales, with particular reference to the grazing factor. *Aust. J. Agric. Res.* **4**: 1-28.

Bodenheimer, F. S. (1951).—"Insects as Human Food." 352 pp. (Dr. W. Junk: The Hague.)

Boisduval, J. A. (1838).—"Voyage de découvertes de L'Astrolabe, Première Partie, Lépidoptères." (Paris.)

Campbell, T. G. (1926).—Insect foods of the aborigines. *Aust. Mus. Mag.* **2**: 407-10.

Clark, L. R. (1948).—Observations on the plant communities at "Bundemar," Trangie district, New South Wales, in relation to *Chortoicetes terminifera* (Walk.) and *Austroicetes cruciata* (Sauss.). Coun. Sci. Industr. Res. Aust. Bull. No. 236: 63 pp.

Collins, D. L. (1934).—Iris-pigment migration and its relation to behaviour in the codling moth. *J. Exp. Zool.* **69**: 165-98.

Common, I. F. B. (1952).—Migration and gregarious aestivation in the bogong moth, *Agrotis infusa*. *Nature* **170**: 981-2.

Currie, G. A. (1930-31).—The brown cutworm (*Euxoa radians* Guen.). *Qd. Agric. J.* **34**: 10-16, 138-63, 383-90, 488-95; **35**: 18-33.

Dickson, R. C. (1949).—Factors governing the induction of diapause in the oriental fruit moth. *Ann. Ent. Soc. Amer.* **42**: 511-37.

Fletcher, T. B. (1925).—Migration as a factor in pest outbreaks. *Bull. Ent. Res.* **16**: 177-81.

Froggatt, W. W. (1900).—Caterpillars: The bugong moth (*Agrotis infusa* Boisd.). *Agric. Gaz. N.S.W.* **10**: 1252-56.

Froggatt, W. W. (1902).—Caterpillar plagues, with an account of the potato pest at Windsor. *Agric. Gaz. N.S.W.* **12**: 237-43.

Froggatt, W. W. (1907).—Entomological notes: A fight with climbing cutworms (*Leucania unipuncta*) at Tamworth. *Agric. Gaz. N.S.W.* **18**: 265-8.

Froggatt, W. W. (1910).—Insects which damage saltbush. *Agric. Gaz. N.S.W.* **21**: 465-70.

Froggatt, W. W. (1911).—Caterpillar pest in Ganmain District. *Agric. Gaz. N.S.W.* **22**: 1021-2.

Geiger, R. (1950).—"The Climate Near the Ground." 2nd Ed. (Translation). 482 pp. (Harvard University Press: Cambridge, Mass.)

Griffith Taylor (1911).—Physiography of eastern Australia. Commonw. Bur. Met. Aust. Bull. No. 8: 18 pp.

Hampson, G. F. (1903).—"Catalogue of the Lepidoptera Phalaenae in the British Museum." Vol. IV, 689 pp. (Longmans & Co.: London.)

Helms, R. (1890).—Report of a collecting trip to Mount Kosciusko. *Rec. Aust. Mus.* **1**: 11-16.

Hounam, C. E. (1947).—Climate of the south west wheat belt of N.S.W. with special reference to rainfall over marginal areas. Commonw. Bur. Met. Aust. Pamph. No. 2: 22 pp.

Hounam, C. E. (1950).—Climate of the north west wheat belt of N.S.W. with special reference to rainfall over marginal areas. Commonw. Bur. Met. Aust. Pamph. No. 4: 31 pp.

Kennedy, J. S. (1951).—The migration of the desert locust (*Schistocerca gregaria* Forsk.) I. The behaviour of swarms. II. A theory of long-range migrations. *Phil. Trans.* B **235**: 163-290.

Lack, D., and Lack, E. (1951).—Migration of insects and birds through a Pyrenean pass. *J. Anim. Ecol.* **20**: 63-7.

Langridge, D. F. (1952).—Bogong moth. *Aust. Bee J.* **33**: 205.

Larsen, E. B. (1949).—Activity and migration of *Plusia gamma* L. Studies on the activity of insects. III. *Biol. Medd., Kbh.* **21**: 1-32.

Leithhead, D. (1951).—Above the tree line. *Wild Life* 13: 459-66.

Lyon, A. V. (1925).—Problems of the viticultural industry. Coun. Sci. Industr. Res. Aust. Bull. No. 28: 84 pp.

McCarthy, T. (1945).—The bugong moth (*Agrotis infusa*). *Agric. Gaz. N.S.W.* **56**: 2.

McKeown, K. C. (1935).—"Insect Wonders of Australia." 252 pp. (Angus & Robertson: Sydney.)

McLuckie, J., and Petrie, A. H. K. (1927).—The vegetation of the Kosciusko Plateau. i. The plant communities. *Proc. Linn. Soc. N.S.W.* **52**: 187-221.

Moore, C. W. E. (1953).—The vegetation of the south-eastern Riverina. II. The disclimax communities. *Aust. J. Bot.* **1** (3): 548-67.

Newman, L. J. (1927).—Army worms, cut worms and web worms. *J. Dep. Agric. W.A.* **4**: 227-39.

Olliff, S. (1890).—The maize moth (*Heliothis armigera*). *Agric. Gaz. N.S.W.* **1**: 125-8.

PATTON, R. T. (1953).—Ecology of the Bogong High Plains. *Vict. Nat.* **69**: 137-42.

PEPPER, J. H. (1932).—Observations on a unidirectional flight of army cutworm moths and their possible bearing on aestivation. *Canad. Ent.* **64**: 241-2.

PRYOR, L. D. (1938).—The botany, forestry and zoology of the Australian Capital Territory on an ecological basis. Aust. N.Z. Ass. Advanc. Sci. Handbook for Canberra, pp. 88-110. (Govt. Printer: Canberra.)

SCOTT, A. W. (1873).—On the "*Agrotis vastator*," a species of moth, now infesting the seaboard of New South Wales. *Trans. Ent. Soc. N.S.W.* **2**: 40-8.

SNOW, D. W., and ROSS, K. F. A. (1952).—Insect migration in the Pyrenees. *Ent. Mon. Mag.* **88**: 1-6.

TURNER, A. J. (1920).—A revision of the Australian Noctuidae. *Trans. Roy. Soc. S. Aust.* **44**: 120-89.

WALKDEN, H. H. (1950).—Cutworms, armyworms and related species attacking cereal and forage crops in the Central Great Plains. U.S.D.A. Circ. No. 849: 52 pp.

WAY, M. J., and HOPKINS, B. A. (1950).—The influence of photoperiod and temperature on the induction of diapause in *Diataraxia oleracea* L. (Lepidoptera). *J. Exp. Biol.* **27**: 365-76.

WILLIAMS, C. B. (1930).—"The Migration of Butterflies." 473 pp. (Oliver and Boyd: Edinburgh.)

WILLIAMS, C. B. (1945).—Notes on the fat content of two British migrant moths (Lepidoptera). *Proc. R. Ent. Soc. Lond.* **A 20**: 6-13.

WILLIAMS, C. B. (1949).—Migration in Lepidoptera and the problem of orientation. *Proc. R. Ent. Soc. Lond.* **C 13**: 70-84.

WILLIAM, C. B. (1951).—Seasonal changes in flight direction of migrant butterflies in the British Isles. *J. Anim. Ecol.* **20**: 180-90.

WILLIAMS, C. B., COCKBILL, G. F., GIBBS, M. E., and DOWNES, J. A. (1942).—Studies in the migration of Lepidoptera. *Trans. R. Ent. Soc. Lond.* **92**: 101-283.

WILTSHIRE, E. P. (1946).—Studies in the geography of Lepidoptera. III. Some Middle East migrants, their phenology and ecology. *Trans. R. Ent. Soc. Lond.* **96**: 163-82.

EXPLANATION OF PLATES 1-4

PLATE 1

Fig. 1.—Part of the granite outcrops at the summit of Mt. Gingera (6092 ft) where most of the observations on aestivating *A. infusa* moths were made.

Fig. 2.—A continuous imbricated layer of *A. infusa* moths on the roof of a cave at Mt. Gingera, A.C.T., January 7, 1953.

PLATE 2

Fig. 1.—*A. infusa* moths clustered in the hollow of a tree trunk, November 5, 1952, when the moth population reached a maximum at the Little Ginini camp, A.C.T.

Fig. 2.—Aestivating moths clustered on the darker side of a thermohygrograph removed from the chief observation cave, Mt. Gingera, A.C.T., January 7, 1953.

PLATE 3

Fig. 1.—A dense stand of *Medicago* sp. with some *Capsella bursa-pastoris* Moench. in a perennial grass pasture on a self-mulching soil near Yetman, northern New South Wales. Larvae of *A. infusa* were very abundant in these pastures in late August 1952.

Fig. 2.—Damage to a crop of linseed caused by larvae of *A. infusa* in the winter of 1952, near Yetman, northern New South Wales. Other similarly damaged patches were scattered throughout the crop.

PLATE 4

Successive flashlight photographs of a group of aestivating moths taken in the afternoon and evening of February 13, 1953, Mt. Gingera, A.C.T., showing depletion due to dispersal.

Fig. 1.—4 p.m., before the period of evening activity.
Fig. 2.—7.40 p.m., after crawling activity had begun.
Fig. 3.—8.20 p.m., when the flight had almost ended.
Fig. 4.—9 p.m., residue of moths after all activity had ended.

THE SOIL-INHABITING NEMATODES OF MACQUARIE ISLAND

By J. S. Bunt*

[*Manuscript received December* 12, 1953]

Summary

The numbers of free-living nematodes in more than 40 Macquarie I. soils were recorded at three different times during the year. The principal conditions affecting the populations have been discussed and it is concluded that the numbers and types of algae and bacteria in the soil are of major importance since most of the nematode species identified are believed to feed on these groups of microorganisms. An attempt has been made to assess the relative importance of nematodes in processes of decomposition in Macquarie I. soils.

I. Introduction

The study of free-living nematodes in the soils of the Antarctic and sub-Antarctic appears to have been neglected in the past and only isolated records have been made of free-living freshwater forms by Certes (1889), von Linstow (1892), and De Man (1904). This is not surprising as it was not until 1942 that the first strictly quantitative study of these organisms in the soil was begun by Franz (1942) in Austria and Overgaard (1949) in Denmark, although a large amount of qualitative and taxonomic work has been undertaken prior to this date in various parts of the world.

An attempt has been made in this paper to evaluate in general terms the importance of these organisms under the relatively severe conditions offered by a range of sub-Antarctic soils. The data were gathered by the author as part of a general soil microbiological survey whilst he was a member of the 1951-52 party of the Australian National Antarctic Research Expedition stationed at Macquarie I.

II. Methods

(*a*) *Soil Sampling*

In August, September, and February 1951-52 soil samples were collected from 42 different localities considered to be reasonably representative of the range of environments occurring on Macquarie I. Where possible, the samples included the surface 6 in. of soil taken from a number of points in each locality. In the field, the soil was carried in cloth bags, being transferred in the natural moist state to glass bottles on return to base camp. The bottles were stored in the dark at room temperature (usually ranging from 0 to 10°C).

---

* Antarctic Division, Department of External Affairs, Melbourne; present address: Microbiology Laboratories, School of Agriculture, University of Sydney.

(*b*) *Separation of the Nematodes from the Soil*

The technique used was unavoidably crude. Ten g of soil was weighed, transferred to a square of fine muslin, and then placed in contact with water warmed to 40°C in a filter funnel fitted with a short clamped length of rubber tubing. After standing for 12 hr, the water, now cold, was run into a clean petri dish. The number of nematodes found in 100 low-power microscope fields, equivalent to 0·2 g soil, was recorded.

III. Description of the Soils

Although a strict pedological study has not been undertaken, certain information has been published by Piper (1938) and Mawson (1943) from analyses returned by the Australasian Antarctic Expedition (1911-14) and the B.A.N.Z.A.R. Expedition (1929-31). More recently, Taylor (A.N.A.R.E. Reports, Series B, in press) has made an intensive ecological study of the island and has shown the close relation that exists between plant association and the character of the underlying soil. As the distribution of the flora is largely controlled by exposure to wind and the position of the water-table, these two factors have a fundamental influence on the types of soil developed. For a general account of Macquarie I., reference should be made to a report by Mawson (1943) of the geography and geology and to the book "Home of the Blizzard," by the same author (1915).

The Macquarie I. plateau is covered by a mantle of glacial till and on the higher areas is quite bare of vegetation. The soil is primitive, low in organic matter, constantly wet, often boggy, frequently frozen, at least at the surface, and the pH lies in the range 5·4-6·9 in the areas sampled for microbiological studies. In all but the most exposed situations the till is dotted with small cushions of the moss *Dicranoweisia antarctica* (C. Müll.) Par. which causes localized increases in the organic matter level in the soil. *Azorella selago* Hook. f., a vascular species, which is only slightly more restricted in its distribution than the moss, forms dense cushions more or less resistant to the wind. These cushions form an incomplete cover over the till and accumulate and protect localized pockets of dark brown peaty material which might be likened to the upper A horizon of more normal soils. The lower, more sheltered parts of the plateau where the plant cover is complete have been designated subglacial herbfield. The species comprising this association form highly organic wet to waterlogged soils several feet thick which overlie the glacial till. The subglacial herbfield also occurs on certain parts of the coast, commonly forming boggy peats up to 15 ft thick.

The wet tussock grassland occupies the steep slopes leading up to the plateau and most of the narrow coastal belt. It is dominated by *Poa foliosa* Hook.f. and *Stilbocarpa polaris* A. Gray, which grow luxuriantly in these situations, forming peats about 4 ft deep on the slopes and characteristic bogs (Cheeseman 1919) on the coast.

In the maritime communities, three species are prominent. *Poa hamiltoni* T. Kirk is commonly found on the rocks in the rookeries of the rockhopper

TABLE 1

DESCRIPTIVE DATA RELATING TO TYPICAL MACQUARIE I. SOILS

Ecological Environment	Elevation (ft)	Water in Samples, O.D. Basis (%)			Soil Temp. Feb. (°C)	pH	Organic C, O.D. Basis (%)	Total N, O.D. Basis (%)	C/N Ratio
		Aug.	Sept.	Feb.					
Glacial till—no plant cover ..	700-800	21-38	23-33	25-33	4·8-5·6	5·4-6·9	2·10-3·20	0·21-0·22	9·5-15·2
Glacial till—*Dicranoweisia antarctica* (C. Müll.) Par. association ..	800	98	53	43	3·8	6·8	3·60	0·30	12·0
Organic soil—*Azorella selago* Hook.f. association	700	143	250	233	4·8	6·2	12·50	0·78	16·0
Upland subglacial herbfield, peat ..	500-650	630-770	500-575	400-566	5·4-6·0	5·4-7·1	18·50-24·10	1·56-2·19	11·0-11·9
Lowland subglacial herbfield, peat	30-40	1000-3000	800-1250	900-1900	7·0-9·0	4·7-6·6	39·4	1·79	22·0
Poa foliosa Hook.f. association of slopes, root masses	150-600	95-544	271-533	300-567	5·3	4·0-5·2	43·6-44·6	3·33	13·1-13·4
Poa foliosa association of slopes, peat between tussocks ..	150-600	318-691	138-700	400-900	5·9	4·0-6·6	—	—	—
Poa foliosa association of coast, root masses	10-20	15-300	12-250	5-186	7·2	4·3-6·8	†1·30	†0·11	†11·8
Poa foliosa association of coast, between tussocks	10-20	12-179*	12-283	18-400	9·4	4·3-5·3	†0·70	†0·16	†4·4
Cotula plumosa Hook.f. society, dark mineral sand	10	8-14	5-8	5-11	7·9-11·0	4·8-7·0	—	—	—
Gentoo penguin rookery ..	40	—	550-567	900	5·0-8·4	5·0-9·2	—	—	—
Rockhopper penguin rookery ..	10	337	186	186	8·0	6·8	—	—	—
Poa hamiltoni T. Kirk root mass ..	10	333	325	300	8·8	3·9	—	—	—
Puccinellia macquariensis Cheesem. root mass	5-10	150	280	82	8·2	6·7	4·4	0·69	6·4
Colobanthus muscoides Hook.f. cushions	5-10	490	600	300	8·8	7·2	—	—	—
Creek bed in wet tussock grassland	250	143	115	233	7·0	6·0	—	—	—

* Figures low because mud in sink holes was avoided.

† Figures low because analyses from area where tussocks growing directly in sand.

penguin (*Eudyptes chrysocome* Miller) and usually grows in small clumps, the restricted but dense root mass embedded in pockets of muddy organic material often rich in penguin excreta. *Puccinellia macquariensis* Cheesem. has a similar habit but grows in more open situations where the rocks are often bathed in sea spray. The "soil" held by the roots is generally rather sandy in nature. *Colobanthus muscoides* Hook.f., an associate of the *Puccinellia*, forms dense cushions on the rocks and the samples taken consist of the partly decomposed material in the interior of the cushions. *Cotula plumosa* Hook.f. also appears on the rocks but is most prominent in pure societies growing in sand at the edge of the littoral on open beaches. This is especially noticeable on the isthmus area between Wireless Hill and the main body of the island.

Further samples were collected from a new rookery formed by gentoo penguins (*Pygoscelis papua* Forster) on a deep peat area covered with *Poa foliosa* Hook.f., the above-ground parts of which had been rapidly destroyed by the activities of the birds and also from a small creek in the wet tussock grassland, choked with minor vascular species and mosses. Data concerning the soils examined are summarized in Table 1 from results obtained by the author.

IV. Weather during the Months of Sampling

A full account of the meteorological findings at Macquarie I. may be found in the A.N.A.R.E. Reports, Series D, Vols. I-IV, 1948-51 and in the reports of the Australasian Antarctic Expedition, 1911-14, Series B, Vol. III, issued 1929. Only chosen data for February, August, and September 1951 are presented in Table 2. The data for February 1952 are not yet available.

Table 2

SUMMARIZED WEATHER DATA FOR FEBRUARY, AUGUST, AND SEPTEMBER 1951

Information collected at station on isthmus 20 ft above sea-level. The mean humidity over the period Jan. 1912-Dec. 1914 was 92 per cent.

Month	Temp. (°F)		Mean Hourly Temp. (°F) (1912-15)	Precipitation		Mean Sunshine (hr/day)	Mean Wind Speed (kt)
	Monthly Max.	Mean Min.		Total (points)	No. of Days		
Feb.	49·2	34·6	42·5	292	24	3·1	18·4
Aug.	43·8	24·0	38·0	327	29	1·6	18·6
Sept.	46·8	18·7	38·1	288	30	1·0	27·7

V. Results

The numbers of nematodes in soil samples collected from various localities in August, September, and February 1951-52, are presented in Table 3. These figures are comparable with the results obtained by other workers with soils from more temperate regions.

It was possible to demonstrate an increase in the population from August to February in only seven of the 13 localities examined. In these, the differences between winter and summer, although slight, were apparently sufficient to influence the reproductive capacity of the nematode population directly by altering the physical environment, or indirectly by altering the food supply, i.e. other soil-inhabiting organisms such as algae and bacteria which might be more sensitive to changes in the soil climate. The figures obtained in the remaining localities do not entirely contradict this tendency. One would not expect a great deal of variation under the severe environmental conditions prevailing in the feldmark, and in the *Cotula plumosa* society a limit to the population would be imposed by the sandy nature of the soil with its low moisture-holding capacity and poor supply of food. No obvious explanation can be found for the irregular results obtained with the September samples from the upland herbfields, nor are the factors understood which appear to be limiting the creek-bed population. The principal conclusion that the nematode population tends to increase with the slight seasonal changes from August to February in all situations but the penguin rookeries was demonstrated by an analysis of variance giving $P < 0{\cdot}01$.

TABLE 3

NUMBERS OF NEMATODES IN SURFACE 15 CM IN A NUMBER OF MACQUARIE I. SOILS AT DIFFERENT TIMES OF THE YEAR

Locality	No. of Sampling Areas per Locality	No. of Nematodes/m$^2 \times 10^{-6}$		
		August	September	February
Feldmark	6	1·80	3·24	2·17
Upland subglacial herbfield	5	2·09	5·91	4·31
Lowland subglacial herbfield	4	2·21	3·77	4·67
Poa foliosa associations (general)	18	3·09	5·98	15·11
Poa foliosa associations of slopes	9	1·70	4·23	7·80
Poa foliosa associations of coast	9	4·13	0·68	17·47
Gentoo penguin rookery ..	2	—*	80·25	59·70
Rockhopper penguin rookery	1	123·76	31·74	8·90
Poa hamiltoni root mass ..	1	5·45	6·80	21·85
Puccinellia macquariensis root mass	1	0·27	2·63	13·06
Colobanthus muscoides cushions	1	6·87	22·09	29·68
Wet creek bed choked with vegetation	1	0·73	2·84	2·20
Cotula plumosa society	2	3·17	0·75	4·83

* No record.

The trends in the penguin rookeries are interesting and, to a certain extent, mutually distinct. The gentoo rookery was established during September 1951 in previously undisturbed *Poa foliosa* associations bordering the lowland herbfields and was occupied by several hundred birds that began to destroy the above-ground portions of the tussocks and lay bare the peaty soil. By February 1952, the rookery had been deserted and the tussock was almost completely destroyed. If one assumes the normal nematode population of the *Poa foliosa* associations to have been about $4 \times 10^6/\text{m}^2$ during September, it will be seen that the penguins caused a 20-fold increase in the numbers of nematodes after 4 weeks on the area. This remarkable increase in numbers was probably caused by a multiplication of the soil bacteria in response to excrement deposited in considerable amounts by the penguins. The further possibility of localized increases in the soil temperature directly beneath the nesting birds favouring the nematodes should not be overlooked. The penguins had not long left the rookery when the February soil samples were collected but the nematode population was still found to be high.

TABLE 4

NEMATODE POPULATIONS WITHIN SEVERAL PLANT ASSOCIATIONS (No./100 g SOIL)

Plant Association or Environment	Local Situation	
	Peat or Mineral Soil Free of Roots	Peaty Material Rich in Roots
Feldmark	700	5,300
Poa foliosa associations (slopes)	15,016	10,084
Poa foliosa associations (coast) ..	5,071	16,898

The rockhopper penguin nests in large numbers on the rockier parts of the coast and in the rookeries it is usual to find considerable amounts of mud washed from neighbouring slopes mixed with feathers and excrement to form putrefying deposits in every rock cavity. During August, when the rookeries were unoccupied, the nematode population was $124 \times 10^6/\text{m}^2$. The numbers had dropped to $32 \times 10^6/\text{m}^2$ at the end of September, when the breeding season was about to commence. By the following February, when the penguins were preparing to leave again, the population had fallen to only $9 \times 10^6/\text{m}^2$ (Fig. 1). By April or May, the rookeries would be deserted. Apparently conditions become unsuitable for the nematodes while the penguins are present in large numbers and it is only after their departure that the population begins to increase. In this habitat, bacteria probably constitute the most important source of food and since the bacterial numbers were found by total count to be almost equal in August and February (2200×10^6 and 2800×10^6/g respectively) it must be assumed that some factor other than food supply limits the build up of nematodes during the penguin breeding season.

The wide variation in the numbers of nematodes occurring in the localities examined is a reflection of the diversity of the physical characters of the soils and of the qualitative and quantitative differences in the composition of the soil microflora and fauna. The type of plant association in any given area may also be important since some of the nematodes live on plant juices and may be selective in their feeding habits. The range in results could not have occurred by chance since an analysis of the variation between localities showed that $P = 0{\cdot}01$. Table 4 shows the numbers of nematodes recorded from different situations within several plant associations. In two localities the numbers are appreciably higher in samples rich in plant roots than in those either with few or none. In the third locality the numbers were similar in both situations. As the plant root feeders do not appear to be of great importance on Macquarie I.,

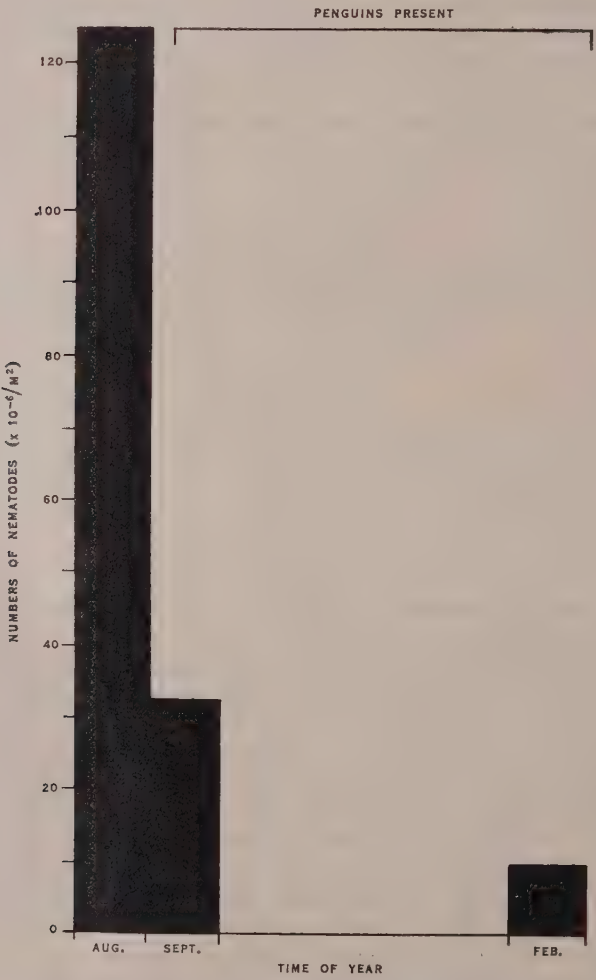


Fig. 1.—Depression of nematode population in the mud of a rock-hopper penguin rookery during the breeding season.

the pattern indicated in Table 4 is probably an indirect effect of plant growth. In the feldmark, food supplies are limited in the bare glacial till so that one would expect a larger micropopulation associated with the moss pads and the *Azorella selago* cushions. More favourable moisture conditions and greater numbers of algae (unpublished data) in the peat between the tussocks as well as a slightly higher soil temperature are probably responsible for the larger nematode population in this situation than in the tussock root masses amongst the *Poa foliosa* associations of the slopes. One might expect a similar condition in the *Poa foliosa* associations of the coast but the physical environment in the root masses is generally more favourable here than in the bogs between the tussocks.

TABLE 5

QUALITATIVE DISTRIBUTION OF NEMATODES IN FIVE TYPICAL MACQUARIE I. SOILS

Species	Species Occurring in Samples				
	Bog Soil Upland Herbfield	Peat. *Poa* Association Coast	Peat. Upland Herbfield	Peat. *Poa* Association Slopes	Bog Peat Lowland Herbfield
Dorylaimus carteri	×		×	×	
Monhystera vulgaris	×	×	×	×	×
Monhystera filiformis?			×		
Prismatolaimus dolichurus	×		×	×	×
Rhabditis sp.	×	×	×	×	×
Plectus cirratus	×			×	
Dorylaimus sp.	×				
Dorylaimus sp.				×	
Monhystera sp.				×	
Teratocephalus terrestris	×				
Cephalobus sp.	×				
Tylenchus sp.			×	×	×
Alaimus sp.			×	×	
Aphelenchoides sp.				×	
Undetermined spp. (12)					

Although only 94 individuals were examined, they give some idea of the qualitative character and quantitative distribution of the species of nematodes in five typical Macquarie I. soils. These findings are presented in Table 5. The common species were *Dorylaimus carteri* Bastian, *Monhystera vulgaris* De Man, *Prismatolaimus dolichurus* De Man, *Rhabditis* sp., and *Dorylaimus* sp. Seven of the species were found in only one soil and only two species were common to every locality. Seven of the 10 listed genera have been recorded by other workers as probable bacterial feeders and all the dominant species belong to this group except *Dorylaimus carteri,* which is a suspected algal feeder. It is clear that the quantitative distribution may be largely dependent upon the character of the microflora in any given environment.

V. DISCUSSION

Although the information available from this study is limited, it should be possible to discuss the principal components of environment influencing the activities of the soil-inhabiting nematodes of Macquarie I. and their probable importance in the soils. It is apparent that the temperature of the soil does not seriously limit the numbers of nematodes since the populations are comparable with those recorded by Overgaard (1949) in Denmark. However, the slightly warmer conditions during the summer months in some instances cause a marked increase in the numbers. It is not possible to judge whether this is a simple temperature response or whether it is the indirect effect of an improved food supply. One would expect temperature to be directly important under the conditions existing in the feldmark, where the ground is frequently frozen but, on the lower parts of the island, the direct effect of temperature appears to be negligible since the numbers of nematodes in the rockhopper penguin rookeries reached their highest levels in midwinter. The assumption that temperature has an indirect effect in controlling the food supply is probably the more correct.

In relation to metabolic activity, temperature appears to have a more direct influence since Overgaard (1949) has shown that *Mononchus papillatus* consumes increasing quantities of oxygen with increasing temperatures up to 27°C. This fact must be considered in assessing the importance of nematodes in sub-Antarctic soils.

Overgaard (1949) considered that the water relations of the soil are not particularly important with organisms as small as nematodes. Here again, the difficulty arises of distinguishing between a direct effect on the organism and an indirect effect on the food supply. It is possible that this factor may be limiting in certain areas where *Poa foliosa* grows in deep wind-blown sand with poor moisture-holding capacity. Most of the soils, however, are continually wet and offer an ideal physical medium for nematode growth. The influence of aeration is associated to some extent with the moisture content of the soil. Although the soils of Macquarie I. generally contain a high percentage of water and are, in fact, frequently or continuously waterlogged, the oxygen tension is probably quite high, as indicated by the common occurrence of yellow or orange oxidized iron compounds in the mineral subsoil below the peat. There are several reasons for this condition. Precipitation usually occurs as fine rain, mist, sleet, and snow and therefore contains large quantities of dissolved oxygen, especially under the prevailing low temperatures. Further, it would appear from observation that the drainage is comparatively rapid in most of the soils so that even where the moisture content is high, continual replacement is taking place. The lower numbers of nematodes in the subglacial herbfields than in the *Poa foliosa* associations may be partly a reflection of differences in the drainage patterns and hence of the oxygen supply in the two types of soil. Under experimental conditions, Overgaard (1949) was able to show no change in the oxygen consumption of nematodes with a 10 per cent. decrease in the oxygen tension.

Some nematodes appear to be tolerant of a wide range of pH conditions. The soils examined varied in pH from 3·9 to 9·2 and high numbers were found at both extremes of the scale. It seems likely that certain substances might sometimes be found under natural conditions to have an inhibitory or toxic influence. The interesting decline in nematode numbers in the rockhopper rookery during the breeding season may be due to such substances in penguin faeces.

Food supply appears to be the most important factor controlling the number of nematodes in the soils of Macquarie I., and from evidence presented by Overgaard (1949), it is probable that the nematodes are largely bacterial or algal feeders. The author has found (unpublished data) that the numbers of algae and bacteria in the soil are much higher in February than in August, the increase varying from 1·5 to 20-fold, and that there are wide quantitative differences in the microflora in different environments. These facts help to explain the differences between the summer and winter nematode population but no relationship could be found between the total nematode population and the total population of bacteria and algae in the various habitats. This is not surprising as it is thought that the soil-inhabiting nematodes may be selective feeders. Selectivity may also exist within the groups of bacterial and algal feeders so that particular species or strains amongst the microflora may be favoured as sources of nutriment. It follows that a large microflora may not be capable necessarily of supporting a large nematode population so that attempts to demonstrate overall relations between nematodes and algae or bacteria are quite likely to fail.

If it be assumed that the amount of oxygen consumed in respiration by any group of soil-inhabiting organisms is proportional to the quantity of organic material decomposed by the group, its relative importance with respect to this function in soil could be estimated. A comparison, in this case, between the nematodes and the total microflora might prove valuable. Overgaard (1949) has related the numbers of nematodes and their total oxygen consumption in 17 soils. The average oxygen consumption was estimated at 3·8 ml/m^2/hr at 16°C and the average population $3{\cdot}6 \times 10^6/\text{m}^2$. The mean population in the Macquarie I. soils during February 1952 was $11{\cdot}3 \times 10^6/\text{m}^2$, excluding the penguin rookeries, and the average soil temperature was approximately 7°C. From the above data it is possible to obtain several estimates for the activity of nematodes in Macquarie I. soils. If it be assumed that the organisms are no less active in these soils than in those of Denmark, it may be calculated that about 12 ml O_2/m^2/hr would be consumed at 7°C. This is considered to be a maximum estimate of activity. A minimum figure may be reached by assuming that activity is directly proportional to temperature, in which case it is found that about 5 ml O_2/m^2/hr at 7°C would be consumed. A more reasonable figure is reached if we assume a degree of adaptability by the nematodes to cold conditions. Such metabolic adaptations have been shown for fish and crustaceans by Scholander *et al.* (1953). Further, Overgaard (1949), working with the nematode *Mononchus papillatus*, has shown that the rate of oxygen consumption is reduced by only 20 per cent. when the temperature is lowered from 16° to 7°C. Using this figure as a working guide, it may be calculated that the Macquarie I. nematode population would consume about 9 ml $O_2/m^2/hr$ at 7°C.

It was found in other studies (Bunt and Rovira 1954) that five typical Macquarie I. soils had a mean oxygen consumption of 22 $\mu l/g$ soil (oven-dry basis)/hr at 10°C (equivalent to about 1 $l/m^2/hr$ at 7°C), principally the result of microbial respiration. Therefore the activity of nematodes is probably only about 0·9 per cent. (estimated range 0·5-1·2 per cent.) of the activity of the microflora in these soils. As the respiratory losses of nematodes far exceed the energy withheld in their tissues (Birch and Clark 1953), these figures should provide a reasonable indication of their importance in relation to processes of decomposition in the soils examined.

VI. ACKNOWLEDGMENTS

The author wishes to thank Mr. D. P. Clark, of the Zoology School, University of Sydney, for examining and naming the nematodes and for his helpful advice and criticism, and Mr. J. M. Vincent, of the School of Agriculture at this University, for suggestions regarding the statistical analysis of the results.

VII. REFERENCES

BIRCH, L. C., and CLARK, D. P. (1953).—Forest soil as an ecological community with special reference to the fauna. *Quart. Rev. Biol.* **28**: 13-36.

BUNT, J. S., and ROVIRA, A. D. (1954).—The effect of temperature and heat treatment on soil metabolism. *J. Soil Sci.* (in press).

CERTES, A. (1889).—Organismes divers appartenant à la faune microscopique de la Terre de Feu. Mission Scientifique du Cap Horn, 1882-3. **6**: 47.

CHEESEMAN, T. F. (1919).—The vascular flora of Macquarie Island. Australasian Antarctic Expedition, 1911-14. Scientific Reports, Series C, Vol. 7, Pt. 3.

DE MAN, J. G. (1904).—"Nématodes Libres. Expédition Antarctique Belge, 1897-9."

FRANZ, H. A. (1942).—Untersuchungen uber die Kleintierwelt ostalpiner, Boden 1. Die freilebenden Erdnematoden. *Zool. Jb.* (1) **75**: 365-546.

MAWSON, D. (1915).—"The Home of the Blizzard." (London.)

MAWSON, D. (1943).—Macquarie Island. Its geography and geology. Australasian Antarctic Expedition, 1911-14. Scientific Reports, Series A, Vol. V.

OVERGAARD NIELSEN, C. (1949).—"Studies on the Soil Microfauna. II. Soil-inhabiting Nematodes." (Naturhistorisk Museum, Aarhus, Danmark.)

PIPER, C. S. (1938).—An examination of soils from Possession, Heard, Kerguelen, and Macquarie Islands. B.A.N.Z. Antarct. Exped. 1929-31, Rep. (A) **2** (7) Sec. 1: 119-24.

SCHOLANDER, P. F., FLAGG, W., WALTERS, V., and IRVING, L. (1953).—Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zoöl.* **26**: 67-90.

TAYLOR, B. W. (1954).—The flora, vegetation and soils of Macquarie Island. A.N.A.R.E. Reports, Series B, Vol. 2, Pt. 1 (in press).

VON LINSTOW, —. (1892).—Helminthen von Süd-Georgien. Nach der Ausbeute der Deutschen Station von 1882-3, Hamburg. *Jb. hamburg. wiss. Anst.* **9**: 2.

ON THE SPECIFIC DISTINCTNESS OF THE OVINE AND BOVINE "STRAINS" OF *HAEMONCHUS CONTORTUS* (RUDOLPHI) COBB (NEMATODA: TRICHOSTRONGYLIDAE)

By F.H.S. Roberts*, Helen Newton Turner†, and Margot McKevett†.

[*Manuscript received January* 29, 1954]

Summary

The investigations reported in this paper were undertaken to determine whether *Haemonchus contortus* from sheep and *H. contortus* from cattle are identical or different species.

The length of the spicules and the distances from the hooks to the tips of the spicules were found to be significantly greater in males from cattle. Differences were also seen in the shape and dimensions of the appendage of the genital cone in males from the two hosts, but these were not constant.

A study of adult females showed at least 14 different types of vulval process. In the majority (88·9 per cent.) of females from sheep there was a long, linguiform process, whereas in the majority (93·5 per cent.) of females from cattle the process was short and rounded. In experimental infestations, despite a change of host, these two types maintained their characteristics in accordance with the host of origin. The progeny of single females from sheep and cattle, respectively, gave a distribution of types similar to that of natural infestations in these hosts.

The infective larvae from the two hosts were found to be visually distinct. Measurements showed significant differences in total length, tail length, and in the ratio of total length to tail length, larvae from cattle having the greater measurements and smaller ratio. A change of host did not alter these differences and no association was apparent between the type of larva and the type of vulval process in the parent female.

In an experiment to test the ability of the two populations to interbreed, mixed sheep and cattle larvae were given to the same host. The subsequent generation of larvae could be classified into sheep and cattle types without any difficulty and there was no evidence of any intermediate types. Evidence of this reluctance to interbreed was also seen under conditions favouring cross-infestation in the field, when both types of larvae maintain their respective characteristics.

In accordance with the above findings and as there is also evidence of some degree of host specificity, it is concluded that the populations in sheep and cattle represent distinct species. The name *Haemonchus contortus* (Rud. 1803) is retained for the species defined in this paper as occurring in sheep and the name *Haemonchus placei* (Place 1893) is proposed for the species occurring in cattle.

I. Introduction

The material on which Rudolphi based his original description of *Haemonchus contortus* was collected from the sheep (Rudolphi 1803). This

---

* Division of Animal Health and Production, C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Qld.

† Section of Mathematical Statistics, C.S.I.R.O., McMaster Laboratory, Sydney.

helminth is now known from most parts of the world and is recorded from all domestic and many species of wild ruminants. It is a common and highly important parasite of cattle, sheep, and goats in Australia, particularly in the northern half of the continent.

The usual description of the female worm refers to a large, linguiform, cuticular process which covers the vulva and extends posteriorly along the body (Ransom 1911; Veglia 1915; de Almeida 1935). Several workers have drawn attention to variations that occur not only in the size and shape of this process (Veglia 1915; Dikmans 1921; de Almeida 1935; Roberts 1941), but also in its position in relation to the vulva (Le Roux 1929; de Almeida 1935). The process may be reduced in size and may sometimes be entirely absent. Frequently it may be placed laterally and sometimes posteriorly to the vulva, and occasionally accessory processes may be present.

The majority of females from sheep have a well-developed, linguiform process, whereas in the majority of females from cattle, this structure is relatively small and rounded (Dikmans 1921; Mönnig 1928; Roberts 1941). It has also been shown that larvae of cattle origin when fed to sheep yield a majority of females with the small, rounded, knob-like process typical of females from cattle and that larvae of sheep origin when fed to cattle yield a majority of females with the long, linguiform type of process typical of females from sheep (Roberts 1941). Another point of interest is the high susceptibility of sheep to larvae from cattle and the difficulty of establishing an infestation in cattle with larvae from sheep (Ross 1931; Roberts 1942). Furthermore, it has been noticed that infective larvae from cattle are longer and more robust, and possess a longer and more whip-like tail than larvae from sheep (Roberts, O'Sullivan, and Riek 1952; Keith 1953).

It has been customary to refer to ovine and bovine strains of *H. contortus**. In view of the differences noted above, however, it seemed that these so-called strains may possibly be distinct species and the studies reported in this paper were planned to determine this point.

The senior author is responsible for the experimental work, including measurements of larvae, and also for the views expressed on the taxonomy of the species. The statistical analyses and interpretations of the data were carried out by the other authors, one of whom (H.N.T.) also provided the contributions on the genetic aspects of the problem.

II. The Adult Worm

In his revision of the genus *Haemonchus,* de Almeida (1935) recognized seven valid species, namely *H. contortus* (Rud. 1803) from the ox, sheep, goat, camel, and many wild ruminants and world-wide in its distribution; *H. longistipes* Railliet and Henry 1909 from the camel and sheep in Asia and Africa; *H. similis* Travassos 1914 from the ox and sheep in Europe, North America, India, Brazil, and Korea; *H. lunatus* Travassos 1914 from the ox in Brazil;

---

* Where the term "strain" has been retained by the authors in the experimental sections of this paper, it is used only as a means of reference to the origin of larvae and adults.

H. bedfordi Le Roux 1929 from a number of wild ruminants in South Africa; *H. mitchelli* Le Roux 1929 from the eland, *Taurotragus oryx* (Pallas) in South Africa; and *H. vegliai* Le Roux 1929 from the kudu, *Strepsiceros strepsiceros* (Pallas), also in South Africa. To these, Gutteres (1949) added *H. santomei* from the ox in Africa. The description of *H. santomei* by Gutteres relies on a cuticular swelling in the region of the head to distinguish this species from *H. contortus*. The females of the other species are difficult to separate, but the males can be recognized by differences in the structure of the bursa and by the spicules.

TABLE 1

MEASUREMENTS OF SPICULES OF ADULT MALE *H. CONTORTUS* FROM SHEEP AND CATTLE

Measurement	Host	No. of Males Measured	Mean Value (μ)	Standard Error of Mean* (μ)	Standard Deviation of a Single Measurement	
					Within Lots (μ)	Including Between-lot Component (μ)
Length of spicule	Sheep	200	424	3·09	22·7	23·7
	Cattle	200	465	2·05	25·1	25·2
Right hook to tip of spicule	Sheep	100	41	0·53	4·2	4·2
	Cattle	100	53	1·04	4·3	4·8
Left hook to tip of spicule	Sheep	100	21	0·37	2·8	2·9
	Cattle	100	28	0·33	3·3	3·3

* Including between-lot component of variance.

(*a*) *Examination of Adult Worms*

The material studied in the present paper was collected from many localities in Queensland. Some of it had been preserved in alcohol, but fresh material was also available.

All the specimens conformed to the description of *H. contortus* as published by Ransom (1911), Veglia (1915), and de Almeida (1935). A close watch was maintained for other species, particularly for the very widely distributed *H. similis*.

(i) *The Male*.—The only structures which yielded any promise of morphological differences between the males from cattle and those from sheep were the spicules and the genital cone.

The spicules were identical in structure, but measurements showed some differences between the strains. Length of spicule was measured on 200 males of each strain, and distance from hook to tip for each spicule on 100 males of each strain. Mean values with their standard deviations are given in Table 1, and the frequency distributions of the lengths are shown in Figure 1. There is considerable overlapping of individual values but for all three measurements the differences between the strain means are significant at the 0·1 per cent. level.

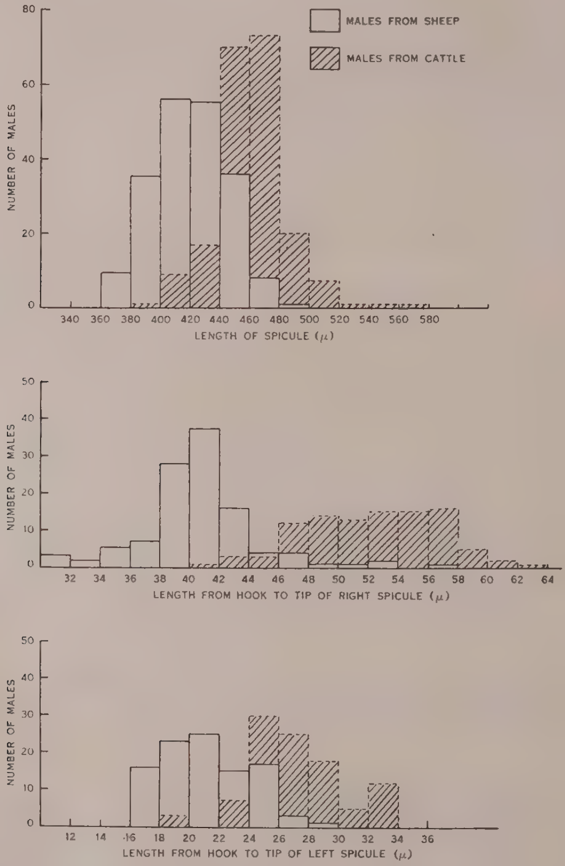


Fig. 1.—Histograms of the frequency distributions of measurements of the spicules of adult males from sheep and from cattle.

The males for which full spicule measurements were available came from ten different lots, five for each strain. Those for which only length of spicule was measured come from two additional lots per strain, 50 from each. The only significant lot differences found were for length of spicule in sheep and for distance from right hook to tip of spicule in cattle. The lot means for the sheep strain ranged from 410 to 434 μ in length, from 40 to 43 μ in distance from right hook to tip, and from 21 to 22 μ in distance from left hook to tip. For cattle, the ranges were from 460 to 474 μ in length, from 52 to 54 μ in distance from right hook to tip, and from 26 to 28 μ in distance from left hook to tip. The strain differences are thus greater than any lot differences within strains.

For 100 males of each strain discriminant function analyses were carried out on the three measurements of the spicule to find whether there was a combination of the measurements which would increase the precision of discriminating between the two strains. The discriminant function found was:

$$D = 3\cdot08 \times (\text{spicule length}) + 26\cdot84 \times (\text{distance right hook to tip}) + 30\cdot35 \times (\text{distance left hook to tip}),$$

where D is the discriminating score combining the three measurements. The probability of misclassification using this function is 0·04, whereas the probability of misclassification for each measurement separately is:

Spicule length, $P = 0\cdot19$; distance right hook to tip, $P = 0\cdot09$; distance left hook to tip, $P = 0\cdot13$.

The combined measurements thus discriminate between the strains with greater precision than any single measurement. This fact is of interest, as it emphasizes the lack of correlation within a strain between length of spicule and the distances from hook to tip. The correlation coefficients between length and the respective distances of hook from tip in the two strains are:

Sheep: Right hook distance × length, $r = -0\cdot06$;
Left hook distance × length, $r = -0\cdot19$.
Cattle: Right hook distance × length, $r = +0\cdot14$;
Left hook distance × length, $r = -0\cdot08$.

These coefficients are all negligible. Within a strain, therefore, longer spicules do not automatically have larger distances from hook to tip, and the greater hook to tip distances in the cattle strain become an additional distinguishing feature and not one which might be considered to follow automatically from the increased spicule length.

The first series of males which was examined to test the value of the genital cone as a specific character was the progeny of a single female from cattle established in a calf and the progeny of a single female from sheep established in a lamb. In the former, the appendage of the genital cone was by comparison uniformly small and stout, measuring 8-10 μ in length and about as long as or, at most, only a little longer than broad. In contrast, this appendage in the males from the lamb measured 13-20 μ in length and was at least one and one-half times as long as broad. These measurements were made on fresh material.

When, however, males were examined from natural infestations of cattle and sheep the differences in the dimensions of this structure were not so clear, as a small percentage of males from sheep exhibited a short, cattle-type appendage and in a small percentage of males from cattle the appendage approached the more elongate, sheep type.

(ii) *The Female.*—A careful study of the female worms indicated that the cuticular process in the region of the vulva was the only character worth serious consideration. It had been noted that a small, rounded process predominated in females from cattle whereas a long, linguiform process predominated in females from sheep, and furthermore that females with a small, rounded process remained in the majority in experimental infestations in which sheep had been fed larvae from cattle and vice versa (Roberts 1941). Studies were accordingly undertaken to test the distribution of the various types of vulval process in the two strains occurring naturally, and also among descendants of a single female of each strain following experimental infestation.

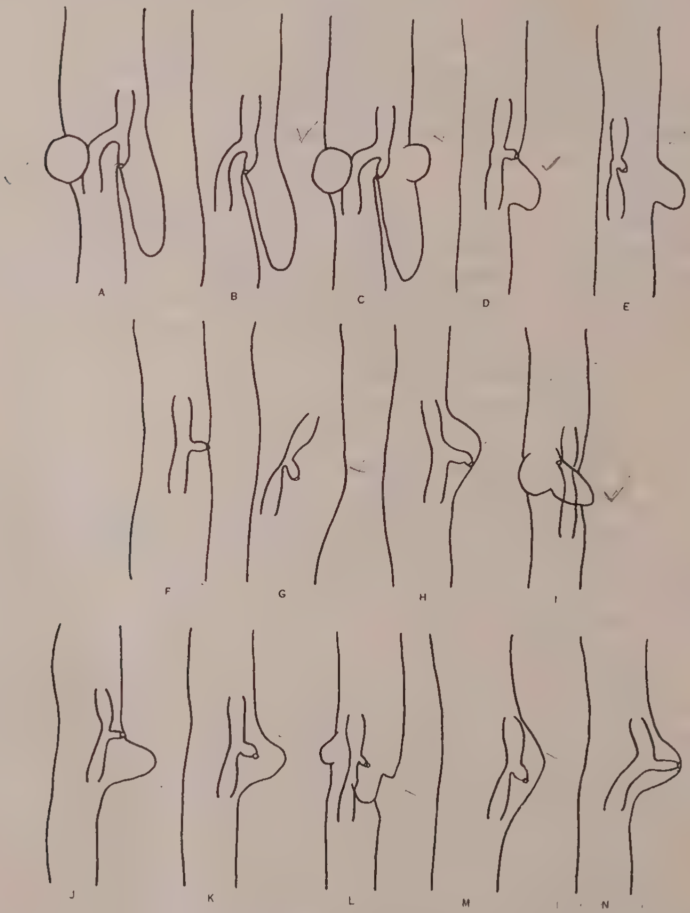


Fig. 2.—Types of vulval process in females from natural infestations in sheep and in cattle.

A large series of female worms from both hosts and from many localities was examined and the main types of vulval processes seen are shown in Figure 2 (types *A-N*). In addition to these, there was a number of intermediate types. Types *D* and *E* show the appearance of the process observed in the majority of females from cattle. About 40 per cent. of these females had the process placed at varying distances laterally to the vulva as in type *E*; in the others the process was ventral and immediately posterior to the vulva as in type *D*. Type *B* shows the process seen in the majority of females from sheep but sometimes accessory processes were present as in types *A* and *C*. The percentages of the various types among the worms examined are shown in Table 2.

TABLE 2

VARIATIONS IN THE VULVAL PROCESS OF *H. CONTORTUS* IN NATURAL INFESTATIONS

Based on the types in Figure 2

Host of Origin	Lot	No. of Adult Females Examined	Percentage with Given Type of Vulval Process			
			A, B, or *C*	*D* or *E*	*H*	Other Types
Sheep	1	400	89·2	0·4	6·3	4·1
	2	320	88·3	0·7	3·4	7·6
	3	500	92·4	1·2	3·7	2·7
	4	210	90·6	0·3	5·2	3·9
	5	500	84·7	1·7	4·9	8·7
	Mean		88·9	1·0	4·7	5·4
Cattle	1	500	3·4	95·0	0·3	1·3
	2	420	4·1	95·2	0·2	0·5
	3	120	2·8	93·4	1·0	2·8
	4	650	5·4	90·2	2·2	2·2
	5	250	1·0	96·2	1·8	1·0
	Mean		3·9	93·5	1·1	1·5

The inheritance of this character was tested by infesting a worm-free calf with larvae from a single selected, cattle-strain female and a worm-free lamb with larvae from a single selected, sheep-strain female. The infestations were built up by autoinfestation, the animals being subsequently killed, the female worms collected, and the types of vulval process determined. The results of this experiment are expressed in Table 3.

Of the 1153 females derived from a single type *D* female from cattle, 1076 or 93·3 per cent. possessed the reduced, knob-like process which characterized the parent female. Of these, 60·4 per cent. conformed to the parent in regard to the position of the vulva and in 39·6 per cent. the process was lateral to the vulva. There were also seven females, or 0·6 per cent. of the total females present, with the type of process seen in the majority of females from sheep, and 70, or approximately 6·0 per cent. of the total females present, with vulval processes of six other types.

These figures may be compared with the percentages of the main types seen in natural infestations and given in Table 2. There is a slight decrease in "other types" and in type *H* for the descendants of the single type *B* female, compared with natural infestations, and a slight decrease in the *A*, *B*, and *C* types for the type *D* female, but the main classes show similar proportions in the natural and artificial infestations.

III. The Infective Larva

The methods used for faecal cultures to obtain infective larvae were kept as uniform as possible. Cultures from cattle were set up according to the procedure outlined by Roberts and O'Sullivan (1950). With sheep faeces, the pellets were lightly crushed and half filled a pint, screw-top jar. The cultures were maintained at 26-28°C. The amount of moisture in a culture is highly important as a culture with inadequate moisture yields comparatively few infective larvae which may be small and sometimes malformed. This point was always carefully watched, particularly with cultures of sheep faeces. All measurements were made on larvae from cultures 7-9 days old.

It has been recognized by Australian workers for many years that the infective larva from cattle can be readily distinguished from the infective larva from sheep by its greater length and by its longer and more whip-like tail. A search was made for other characters of possible diagnostic value but none was found. The shape of the stoma at first appeared to be a useful distinguishing character but further work failed to confirm this.

Table 3

VARIATIONS IN THE VULVAL PROCESS OF *H. CONTORTUS* IN DESCENDANTS OF SINGLE FEMALES FROM CATTLE AND SHEEP

Based on the types in Figure 2

Host of Origin	Type of Female	Host Infested	No. of Adult Female Descendants Examined	Percentage with Given Type of Vulval Process			
				A, *B*, or *C*	*D* or *E*	*H*	Other Types
Sheep	*B*	Sheep	545	93·8	1·1	1·8	3·3
Cattle	*D*	Cattle	1153	0·6	93·3	4·0	2·1

(*a*) *Measurements of Infective Larvae from Natural Infestations*

Keith (1953) notes the total body length and tail length for larvae from cattle to be from 749 to 866 μ and from 158 to 193 μ respectively and quotes measurements recorded by various workers for larvae from sheep as from 650 to 751 μ and from 119 to 165 μ respectively.

To ascertain whether there were any significant differences between these measurements for larvae from cattle and sheep, 500 larvae from natural infestations of each host were examined. Each series of 500 larvae was composed of five lots each of 100 larvae and each 100 larvae originated in a different locality. The possibility of sheep larvae appearing in cultures of cattle faeces or vice versa was avoided as far as practicable by restricting faecal samples to herds and flocks where no intermingling of the two hosts was evident. The measurements of the infective larvae are summarized in Table 4, and plotted in Figure 3.

Some of the differences between lots from different localities were found to be significant at the 0·1 per cent. level for all measurements on larvae from both hosts. The lot means for total length ranged from 708 to 752 μ for sheep and from 775 to 807 μ for cattle; for tail length, from 134 to 145 μ for sheep and from 165 to 173 μ for cattle; and for total length-tail length ratio, from 5·13 to 5·41 for sheep and from 4·64 to 4·75 for cattle. The differences between the lots could be due to variations in culture conditions. The grand means of larvae from the two hosts also differed significantly ($P < 0{\cdot}001$) for all measurements, the differences being greater than any differences between lots.

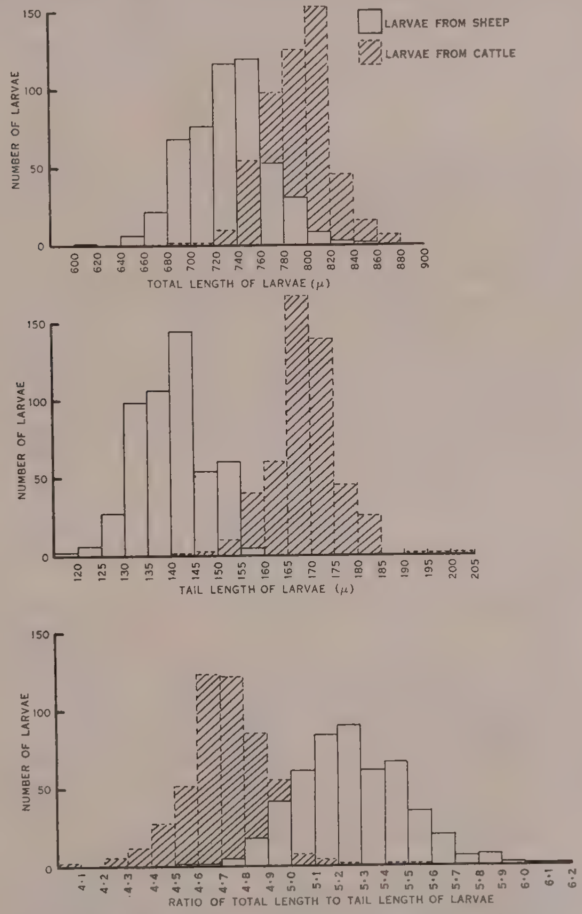


Fig. 3.—Histograms of the frequency distributions of measurements of infective larvae from sheep and from cattle.

Figure 3 shows frequency distributions for the three measurements on larvae from the two hosts, the figures being pooled from all lots. Using the standard deviation from the last column of Table 4, in which differences between lots from different localities are taken into account, it is possible to calculate the probability of misclassification of a larvae, using each of the three measurements. The probability of misclassification on total length alone is 0·18, on tail length alone 0·03, and on ratio alone 0·10.

The possible increase in precision of classifying by some combination of the measurements was investigated by calculating two discriminant functions, one using total length and ratio, and the other using tail length and ratio. The two functions were:

$$D_1 = -0{\cdot}97 \times (\text{total length}) + 167{\cdot}11 \times (\text{ratio}),$$

and

$$D_2 = 5{\cdot}13 \times (\text{tail length}) - 29{\cdot}29 \times (\text{ratio}),$$

where D_1 and D_2 are the discriminating scores combining the other measurements. Using D_1, the probability of misclassification is 0·03, and using D_2 less than 0·02.

The larvae from the two hosts were quite distinct in appearance (Plate 1). Those from sheep were comparatively slender, with the tail of the sheath gradually tapering to end in a fine blunt point, although sometimes extended into a short filament. Those from cattle were more robust, with the tail invariably terminating in a much longer and finer filament. The variation in tail length seen in larvae from cattle is due mainly to variations in the length of this filament. Both types of larvae frequently had a kink in the tail of the sheath immediately posterior to the tail of the larva proper.

TABLE 4

MEASUREMENTS OF INFECTIVE LARVAE OF *H. CONTORTUS* FROM NATURAL INFESTATIONS OF SHEEP AND CATTLE

Measurement	Host	No. of Larvae Measured	Mean Value	Standard Error of Mean*	Standard Deviation of a Single Measurement	
					Within Lots	Including Between-lot Component
Total length	Sheep	500	732 μ	9·6 μ	28·0 μ	35·1 μ
	Cattle	500	793 μ	6·4 μ	24·4 μ	28·1 μ
Tail length	Sheep	500	140 μ	1·9 μ	6·2 μ	7·5 μ
	Cattle	500	168 μ	1·6 μ	6·4 μ	7·2 μ
Ratio $\frac{\text{Total length}}{\text{Tail length}}$	Sheep	500	5·25	0·05	0·21	0·24
	Cattle	500	4·72	0·02	0·17	0·18

* Including between-lot component of variance.

(*b*) *Relationship between Type of Female and Type of Larva*

The study of larvae from natural infestations showed a few larvae from cattle with comparatively short tails and with a body length-tail length ratio approaching that of larvae from sheep. There were also a few larvae from sheep with comparatively long tails and a body length-tail length ratio approaching that of cattle. It seemed that these larvae might be associated with the type of female, those with short tails from cattle with females of type *B* (Fig. 2) and those with long tails from sheep with females of type *D* or *E* (Fig. 2) occurring naturally in cattle and sheep respectively. Accordingly, cultures were set up of eggs from single females of those two types from both hosts and their larvae were isolated and examined. The results are summarized in Table 5.

TABLE 5

RELATIONSHIP BETWEEN THE TYPE OF FEMALE *H. CONTORTUS* AND THE TYPE OF LARVA

Type of female based on Figure 2

Measurement	Host	Larvae of Female Type *B*		Larvae of Female Type *D*		Pooled S.D.
		No. of Larvae Measured	Mean Measurement	No. of Larvae Measured	Mean Measurement	
Total length	Sheep	50	711 μ	50	707 μ	24·1 μ
	Cattle	50	761 μ	50	763 μ	31·9 μ
Tail length	Sheep	50	135 μ	50	133 μ	6·6 μ
	Cattle	50	159 μ	50	157 μ	7·9 μ
Ratio						
$\frac{\text{Total length}}{\text{Tail length}}$	Sheep	50	5·30	50	5·33	0·24
	Cattle	50	4·80	50	4·84	0·17

No significant differences were found between the larvae from the female with the long, linguiform process and the larvae from the female with the short, stunted process on the three measurements for either the sheep or cattle strain.

(*c*) *Influence of the Host on Type of Larva*

As it seemed possible that the larger, more robust type of larva obtained from cattle could simply be an indication that the parasite enjoyed more favourable conditions in cattle than it did in sheep, some observations were made to determine whether such a host influence existed. This was accomplished by infesting cattle with larvae from sheep and vice versa and studying the larvae produced by these infestations.

(i) *Larvae from Sheep Infested with Cattle-strain Larvae.*—In this experiment a worm-free lamb was given several thousand larvae which were the progeny of a single female from cattle established in sheep since July 1949 at the McMaster Laboratory, C.S.I.R.O., Sydney. When received at Yeerongpilly, this strain had been passed through eight different sheep and the number of generations had been still further increased by autoinfestation of each of these animals. The measurements summarized in Table 6 were obtained from a sample of 100 larvae after an additional generation in a lamb at Yeerongpilly and are compared with measurements of 500 larvae recorded from natural infestations in cattle and summarized in Table 4.

TABLE 6

INFLUENCE OF CHANGE OF HOST ON THE TYPE OF LARVA OF *H. CONTORTUS*

A comparison of measurements of larvae from sheep infested with larvae from cattle and of larvae from natural infestations in cattle

Measurement	Cattle Strain Established in Sheep			Cattle Strain from Natural Infestations in Cattle			Standard Error of Differences*
	No. of Larvae Measured	Mean Measurement	S.D. (within lots)	No. of Larvae Measured	Mean Measurement	S.D. (within lots)	
Total length	100	815 μ	32·2 μ	500	793 μ	24·4 μ	15·6 μ
Tail length	100	169 μ	7·7 μ	500	168 μ	6·4 μ	3·8 μ
Ratio $\frac{\text{Total length}}{\text{Tail length}}$	100	4·82	0·18	500	4·72	0·17	0·05

* Including between-lot component.

No significant difference was observed in total length or tail length between the cattle-strain larvae established in sheep and the cattle-strain larvae from natural infestations. The apparent differences between the means for the total length are within the limits of expectation when the between-lot component calculated for Table 4 is included in the standard error. On ratio, the difference is just significant at the 5 per cent. level, the value for cattle strain established in sheep being higher than the value from natural infestations in cattle. In view of the fact that the difference is just significant, and is, in any case, in the direction of increased total length of larvae in the changed host, it is reasonable to conclude that the environment in the cattle host is not responsible for differences observed between the two strains of larvae in natural infestations.

It is perhaps worth noting that measurements of total length and tail length were significantly more variable for the 100 cattle-strain larvae from sheep than for larvae from natural infestations, as shown from the within-lot deviations given in Table 6.

(ii) *Larvae from Cattle Infested with Sheep-strain Larvae.*—Two worm-free calves were used in this experiment. The first animal received an initial dose of 1000 larvae from sheep and a further 8000 larvae derived from its own infestation 37 days later. The egg count at no time exceeded 60 e.p.g* and was usually 10-30 e.p.g. This animal was killed 70 days after the trial was commenced and yielded 15 females. The second animal received an initial dose of 300 larvae and subsequent doses of 1500, 1200, and 20,000 larvae by autoinfestation, the last dose being given 48 days after the first. The maximum egg count recorded was 200 e.p.g. and thereafter the count rapidly declined. When the animal was killed 15 wk after the trial was commenced the count was only 10-40 e.p.g. and 36 females were present.

---

* e.p.g.: Eggs per g faeces.

The measurements of a sample of the larvae fed to each calf and of larvae subsequently obtained from each calf are summarized in Table 7. Only one culture was made from calf No. 1 and this was at 40 days after the second infestation. Several cultures were made from calf No. 2 and the figures for these are given in Table 8.

TABLE 7

INFLUENCE OF CHANGE OF HOST ON THE TYPE OF LARVA OF *H. CONTORTUS*

Measurements of larvae from cattle infested with larvae from sheep

Measurement	Calf No.	Before Infestation			After Infestation				
		No. of Larvae Measured	Mean Measurement	S.D.	No. of Larvae Measured	Mean Measurement	S.D.	S.D. Including Times* Component	S.E. Including Times* Component
Total length	1	44	730 μ	40·4 μ	50	739 μ	33·0 μ	—	—
	2	50	713 μ	25·8 μ	350	718 μ	27·7 μ	30·1 μ	4·65 μ
Tail length	1	44	136 μ	6·7 μ	50	138 μ	6·2 μ	—	—
	2	50	135 μ	5·0 μ	350	137 μ	6·0 μ	6·4 μ	0·96 μ
Ratio: $\frac{\text{Total length}}{\text{Tail length}}$	1	44	5·35	0·21	50	5·37	0·22	—	—
	2	50	5·30	0·13	350	5·24	0·19	0·21	0·03

* Cultures were made at different times after infestation.

No significant differences were observed in either of the measurements or in the body length-tail length ratio of the larvae before and after infestation.

Table 8 shows the variations that may be expected in measurements among larvae from cultures taken at different times from the same animal. These differences are probably influenced by variations in culture conditions, for example, the type of faeces. The measurements are, however, well within the range of lot means for natural infestations which are discussed in association with Table 4.

(*d*) *Cross-breeding between Adult Worms from Cattle and Sheep*

In view of the significant differences noted above between specimens obtained from cattle and sheep, namely those of length and hook distance in the spicules of males and of body length, tail length, and of the body length-tail length ratio of the larvae, it would appear that there are two distinct species involved. This suggestion is supported by observations on natural infestations when the two hosts have been running together for a number of years and which show that, despite the opportunities for cross-breeding between adult worms, the two types of larvae have remained typical and distinct.

In an experiment to test this possibility, a worm-free lamb was given a mixture of 5000 larvae from sheep and 5000 larvae from cattle. The sheep was selected as the experimental host as it was considered probable that a better response would be given by a lamb to a mixture of larvae than by a calf which could be resistant to larvae from sheep.

TABLE 8

INFLUENCE OF CHANGE OF HOST ON THE TYPE OF LARVA OF *H. CONTORTUS*

Measurements of larvae from cattle infested with larvae from sheep.
Data from calf No. 2

Days after Infestation	No. of Larvae Measured	Mean Measurements: Total Length (μ)	Mean Measurements: Tail Length (μ)	Ratio $\frac{\text{Total Length}}{\text{Tail Length}}$ (Mean Values)
Pre-infestation	50	713	135	5·30
22	50	742	141	5·27
37	50	712	138	5·15
60	50	719	136	5·28
74	50	715	139	5·14
80	50	702	134	5·26
85	50	724	136	5·34
96	50	714	136	5·25
Mean		718	137	5·24

The sheep larvae matured earlier than the cattle larvae and cultures made up to 32 days after infestation yielded sheep-type larvae only. Larvae derived from the faeces of this lamb were examined over a period of 2 months after infestation. The lamb was then killed and 1485 female worms were collected, 31 per cent. of which possessed the long, linguiform, vulval process of sheep-type females (Fig. 2*A*, *B*, *C*) and 60 per cent. the reduced, rounded process of cattle-type females (Fig. 2*D*, *E*).

On each culture date 200 larvae were examined and after they had been classified visually into sheep and cattle types, 50 of each type, if available, were measured. It soon became evident that both types of larvae had become shorter than those used for infestation but, even with unusually short larvae, it was only rarely that any difficulty was experienced in deciding whether they were sheep or cattle type. This decrease in length in both types was possibly associated with variations in culture conditions.

The measurements are summarized in Table 9 which shows the mean measurements for all cultures in which both types of larvae appeared. The proportions of larvae and the mean measurements of each type in each culture are given in detail in Table 10.

Table 9

INTERBREEDING BETWEEN ADULT *H. CONTORTUS* OF SHEEP AND CATTLE ORIGIN

Summary of measurements of larvae from all cultures from a sheep infested with a mixture of larvae from sheep and cattle

Measurement	Type of Larvae	Before Infestation			After Infestation				
		No. of Larvae Measured	Mean Measurement	S.D.	No. of Larvae Measured	Mean Measurement	S.D. of a Single Larva	S.D. Including Times* Component	S.E. Including Times* Component
Total length	Sheep	50	719 μ	23·5 μ	350	679 μ	25·3 μ	32·1 μ	7·6 μ
	Cattle	50	793 μ	22·3 μ	350	732 μ	27·8 μ	36·1 μ	8·8 μ
Tail length	Sheep	50	136 μ	4·6 μ	350	134 μ	6·1 μ	6·8 μ	1·3 μ
	Cattle	50	166 μ	5·8 μ	350	160 μ	7·4 μ	8·5 μ	1·7 μ
Ratio $\frac{\text{Total length}}{\text{Tail length}}$	Sheep	50	5·28	0·18	350	5·08	0·17	0·18	0·02
	Cattle	50	4·77	0·14	350	4·59	0·17	0·18	0·02

* Cultures were made at different times after infestation.

Frequency distributions of total length, tail length, and total length-tail length ratios for the two types of larvae are set out graphically in Figure 4. This graph should be compared with Figure 3, which gives the distributions for natural infestations. It is evident from Figure 4 that the two types of larvae are still distinct. The probability of misclassification on tail length alone is 0·05, on total length alone 0·22, and on ratio alone 0·09. These figures may be compared with those of 0·03, 0·18, and 0·10 respectively, obtained on the natural infestations.

IV. DISCUSSION

This investigation was designed to ascertain whether the differences between the adults and infective larvae of *H. contortus* from sheep and cattle are sufficiently significant to warrant classifying these helminths as distinct species.

The spicules of males from the two hosts showed significant differences in their length and also in the distances from both the right and left hooks to the tip of the spicules, the males from cattle having the larger measurement in all three instances. There was no correlation between hook distance and spicule length among the males from either host so that the increased distances in the males from cattle are an added distinguishing feature.

The appearance and length of the appendage of the genital cone, when studied among the progeny of a single female from cattle and of a single female from sheep, gave considerable promise as a character which could be used to distinguish between males from the two hosts. When, however, extensive examinations were made among natural populations, this character proved less reliable.

TABLE 10

INTERBREEDING BETWEEN ADULT *H. CONTORTUS* OF SHEEP AND CATTLE ORIGIN

Proportions and measurements of larvae in each culture from a sheep infested with a mixture of larvae from sheep and cattle

Days after Infestation	Type of Larvae	Per cent. of Each Type	No. of Larvae Measured	Mean Measurements		Ratio $\frac{\text{Total Length}}{\text{Tail Length}}$
				Total Length (μ)	Tail Length (μ)	(Mean Values)
Pre-infestation	Sheep	—	50	719	136	5·28
	Cattle	—	50	793	166	4·77
24	Sheep	100	50	755	149	5·06
	Cattle	—	—	—	—	—
32	Sheep	100	40	676	131	5·17
	Cattle	—	—	—	—	—
34	Sheep	85	50	669	133	5·03
	Cattle	15	50	735	156	4·70
39	Sheep	22	50	677	134	5·04
	Cattle	78	50	729	160	4·55
46	Sheep	60	50	718	141	5·11
	Cattle	40	50	769	168	4·59
53	Sheep	40	50	659	132	5·00
	Cattle	60	50	696	154	4·52
58	Sheep	25	50	680	131	5·18
	Cattle	75	50	744	161	4·62
65	Sheep	30	50	686	135	5·09
	Cattle	70	50	741	162	4·59
66	Sheep	40	50	662	131	5·07
	Cattle	60	50	713	157	4·56

Observations on the type of vulval process possessed by females from cattle and females from sheep confirmed those previously recorded (Roberts 1941). At least 14 types of vulval process were seen and, whereas 88·9 per cent. of females from sheep had a long, linguiform process, this type of process occurred in only 3·9 per cent. of the females from cattle. On the other hand, 93·5 per cent. of females from cattle had a short, knob-like process, whereas only 1·0 per cent. of females from sheep had this type of process.

The distribution of the various types of vulval processes occurring among the progeny of a single female with a long, linguiform process from sheep and experimentally established in a lamb and of a single female with a short, knob-like process from cattle, experimentally established in a calf, was similar to that found in natural populations in these respective hosts. The single females used as the basis of these infestations could, however, have been fertilized by more than one male and the adult females finally examined could have resulted from random matings for an unknown number of generations. The question of inheritance from a single female could be solved only by confining together in the abomasum of a worm-free lamb or calf a single male and a single female with known type of vulval process collected before mating had occurred and studying the progeny. As, however, when cattle-type larvae are fed to sheep and vice versa, the distribution of at least the more prevalent types of vulval process is

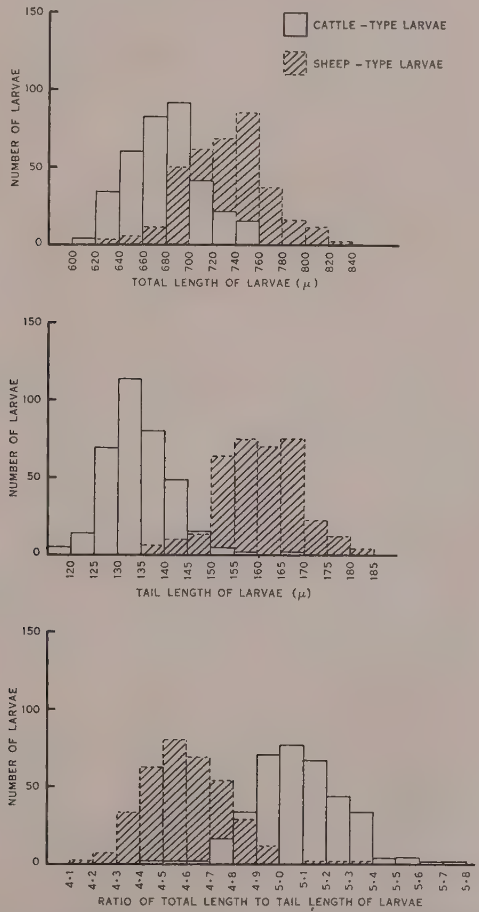


Fig. 4.—Distribution of measurements of first generation infective larvae from an infestation established in sheep from a mixture of larvae from cattle and sheep.

maintained in accordance with the host of origin, it is evident that the type of distribution in each host is not influenced by a change of host and therefore must be inherent.

The infective larvae obtained from naturally occurring infestations in cattle and sheep can be distinguished visually without any difficulty. Significant differences were obtained in measurements of total length, tail length, and also in the ratio of total length to tail length. The distributions of the total length measurements and of the ratio gave some overlapping, but, on tail length measurements alone, the probability of misclassification is only 0·03. A combination of total length and ratio gives a probability of misclassification of 0·03 and combining tail length and ratio, a probability of misclassification of 0·02.

Very marked between-lot differences in total length and tail length measurements were found which are probably associated with nutritional and other effects derived from the culture media. Similar differences were also observed when samples were taken from the same animal at different times. These between-lot differences were taken into account when assessing the significance of differences between the larvae from the two hosts and also when assessing the probability of misclassification. On the present data, tail length alone would differentiate adequately between the larvae from cattle and those from sheep. However, in view of the possibility of an extreme environment having an effect on the larvae much greater than any here recorded, it would be safer to classify on both tail length and ratio of tail length to total length.

It is obvious from the data presented in the paper that the differences between the larvae from cattle and those from sheep are clear-cut and not in any way influenced by the type of vulval process of the parent female or by the species of host. Females with long, linguiform processes obtained from cattle, for example, produced cattle-type larvae and females with short, knob-like processes obtained from sheep produced the smaller sheep-type larvae. Moreover, the larvae of females established in sheep from larvae from cattle maintained their cattle-type characteristics and vice versa.

In the experiments designed to determine the influence of the host on the type of larva, a much greater variability was observed in the measurements of larvae from sheep infested with larvae from cattle than was apparent among larvae from naturally infested cattle. The same degree of variability was seen among the cattle-type larvae obtained from a lamb, when an attempt was made to ascertain whether any cross-breeding occurred between adults of sheep and adults of cattle origin. No such variability was in evidence in any of the larvae from females established in cattle from larvae from sheep, and its significance is unknown.

When the parasites from sheep and cattle are compared, it would appear that there are clear morphological differences between the males and the infective larvae and that, at least with the larvae, the differences override any environmental effects. These differences could have specific value and this suggestion is supported by the distinctive appearance of each type of infective larva. However, any such value that may be considered for the differences in spicule and larval measurements must take into account the degree of overlapping that was recorded for all these measurements.

The absolute test of the validity of any two closely allied but doubtful species is their ability to form a single interbreeding community. With *H. contortus* of cattle and sheep, this could best be accomplished by establishing in the one host males from sheep and females from cattle and vice versa, the worms being collected and transferred before the females had been fertilized by their own type males, and noting the fertility of the infestations and also of their progeny. The cross-breeding experiment attempted by the authors is a compromise and its disadvantages are recognized, one of the chief being that it was carried only to the first generation. In this generation the larvae which were recovered were still of two distinct types and could be separated visually. It is possible to set up a number of genetic models to explain the differentiation into two types in the first generation in the presence of cross-breeding, but without data from later generations none of the models can be tested. The simplest explanation of all has, therefore, been tentatively adopted, namely, that no significant degree of cross-breeding took place. This conclusion is supported by the fact that in natural infestations the two types of larvae maintain their distinctiveness when cattle and sheep are run together over long periods.

It is evident, therefore, that differences exist between specimens of *H. contortus* derived from sheep on the one hand, and from cattle on the other, which are undoubtedly genetic. There is also evidence from the observations of Ross (1931) and of Roberts (1942) of some degree of host specificity. These observations are supported firstly by the difficulty encountered in the present investigation of establishing larvae from sheep in calves, and secondly by the fact that, whereas in the field heavy infestations of cattle origin have been seen on occasions in sheep, infestations of sheep origin in cattle have always been on a low level. It is true that, on the data presented, there is some doubt of the existence of a fertility barrier; nevertheless it is clear that there is at least a reluctance by the two populations to interbreed. Species differentiation, on the basis of fertility barriers, is not always straightforward, for these, whether morphological, physiological, or genetic, are frequently not clearly defined, with the result that a decision becomes a matter of balanced judgement rather than application of a fixed rule. In accordance with these considerations, it is concluded that the data given in this paper strongly support a decision that the two populations represent distinct species.

The name *H. contortus* (Rud.) must be retained for the species defined in this paper as occurring in sheep. For the species from cattle, it would be preferable, if possible, to use the name, other than *contortus,* under which the species was first described from this host. The synonymy of *H. contortus* as set out by Ransom (1911), includes only one such name, *Strongylus placei,* applied by Place (1893) to a helminth which he considered responsible for "anaemic diarrhoea" in calves in South Australia. Place's description of his species is limited to a statement that the worms were found on the mucous membrane of the abomasum of calves and measured 1-3 cm in length. Species representing three genera, namely, *Trichostrongylus, Ostertagia,* and *Haemon-*

chus, occur in the abomasum of cattle in Australia and the range of length given by Place can refer only to *Haemonchus.* It is therefore considered justified to apply the name *Haemonchus placei* (Place 1893) Ransom 1911 to the species of *Haemonchus* discussed in this paper as infesting cattle. It is probable that *H. santomei* Gutteres is a synonym of *H. placei.*

The characters whereby *H. contortus* and *H. placei* may be differentiated are summarized below:

HAEMONCHUS CONTORTUS (Rudolphi) Cobb

Strongylus contortus Rudolphi, 1803.
Haemonchus contortus Cobb, 1898.

Male

Spicules usually less than 440 μ in length, the hook of the right spicule usually less than 44 μ from the tip and the hook of the left spicule usually less than 24 μ from the tip; appendage of genital cone usually at least 1½ times as long as broad.

Female

Vulval process of female usually long and linguiform, as in Figure 2*A, B, C*.

Infective larva

Total length, including sheath, usually less than 760 μ; tail of sheath usually less than 155 μ; ratio of total length to tail length usually greater than 4·9.

Host specificity

Normally in sheep and difficult to establish in cattle.

HAEMONCHUS PLACEI (Place) Ransom

Strongylus placei Place, 1893.
Haemonchus placei Ransom, 1911.

Male

Spicules usually greater than 440 μ in length, the hook of the right spicule usually more than 44 μ from the tip and the hook of the left spicule usually more than 24 μ from the tip; appendage of genital cone usually, at most, only a little longer than broad.

Female

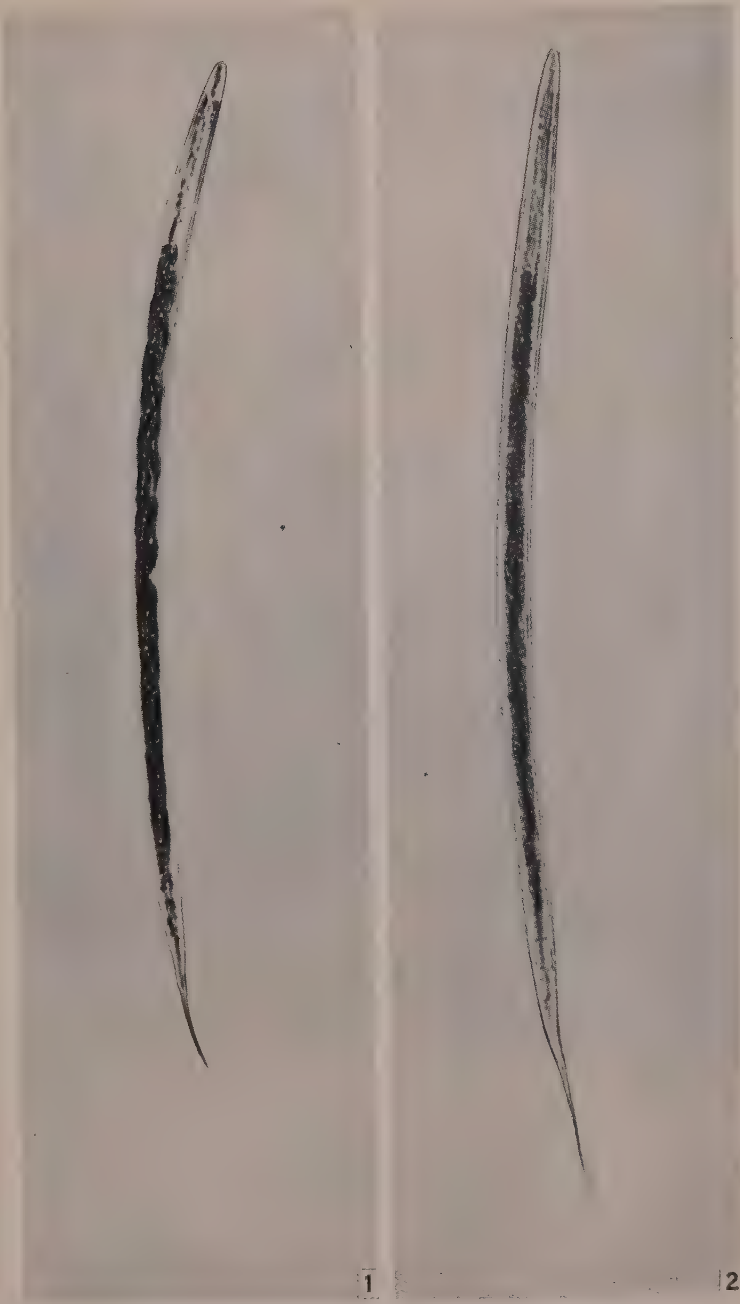
Vulval process of female usually short and rounded as in Figure 2*D, E*.

Infective larva

Longer and more robust and with a longer and more whip-like tail than infective larva of *H. contortus*; total length, including sheath, usually greater than 760 μ; tail of sheath usually greater than 155 μ; ratio of total length to tail length usually less than 4·9.

Host specificity

Normally in cattle, but readily infests sheep.



Infective larvae from natural infestations from (Fig. 1) sheep and (Fig. 2) from cattle, each × 200.

V. Acknowledgments

The authors wish to record their thanks to Mr. H. McL. Gordon, McMaster Animal Health Laboratory, C.S.I.R.O., Sydney, for supplies of infective larvae; to Mr. R. K. Keith and Mr. R. A. J. Meyers, Veterinary Parasitology Laboratory, C.S.I.R.O., Yeerongpilly, for assistance with the figures; and to Dr. J. F. A. Sprent, Faculty of Veterinary Science, University of Queensland, and Dr. I. M. and Dr. M. J. Mackerras, Queensland Institute of Medical Research, for helpful advice in the preparation of the manuscript.

VI. References

Cobb, N. A. (1898).—*Agric. Gaz. N.S.W.* **9**: 419.

de Almeida, J. (1935).—*Mem. Inst. Osw. Cruz.* **30**: 57.

Dikmans, G. (1921).—Preliminary notes on parasites found in ruminants at the Municipal Abattoir, Baton Rouge, Louisiana. Agric. Exp. Sta. Louisiana, Bull. No. 183.

Gutteres, J. de B. (1949).—*Ann. Parasit. Hum. Comp.* **24**: 93.

Keith, R. K. (1953).—*Aust. J. Zool.* **1**: 223.

Le Roux, P. L. (1929).—15th Rep. Dir. Vet. Serv. S. Afr. p. 451.

Mönnig, H. O. (1928).—13th and 14th Rep. Dir. Vet. Serv. S. Afr. p. 801.

Mönnig, H. O. (1931).—17th Rep. Dir. Vet. Serv. S. Afr. p. 225.

Place, F. E. (1893).—*Vet. Rec.* **5**: 589.

Ransom, B. H. (1911).—The nematodes parasitic in the alimentary tract of cattle, sheep and other ruminants. U.S. Dep. Agric. B.A.I. Bull. No. 127.

Roberts, F. H. S. (1941).—*Proc. Roy. Soc. Qd.* **53**: 97.

Roberts, F. H. S. (1942).—*Aust. Vet. J.* **18**: 19.

Roberts, F. H. S., and O'Sullivan, P. J. (1950).—*Aust. J. Agric. Res.* **1**: 99.

Roberts, F. H. S., O'Sullivan, P. J., and Riek, R. F. (1952).—*Aust. J. Agric. Res.* **3**: 187.

Ross, I. C. (1931).—*Aust. J. Exp. Biol. Med. Sci.* **8**: 217.

Rudolphi, C. A. (1803).—*Arch. Zool. Zoot.* **3**: 1.

Veglia, F. (1915).—3rd and 4th Rep. Dir. Vet. Serv. S. Afr. p. 349.

AUSTRALIAN TRIGONALIDAE (HYMENOPTERA: ICHNEUMONOIDEA)

By E. F. RIEK*

[*Manuscript received February* 8, 1954]

CONTENTS

Summary 296
Introduction 296
Family Trigonalidae 297
  Genus *Mimelogonalos* Schulz 297
    Key to species of the genus *Mimelogonalos* 297
  Genus *Taeniogonalos* Schulz 301
    Key to Australian species of the genus *Taeniogonalos* .. 302
References 307
List of species 307

Summary

The paper deals with the taxonomy of the Australian representatives of the Trigonalidae, a family of wasps parasitic on sawflies. Four new species of *Mimelogonalos* and two new species and one subspecies of *Taeniogonalos* are described.

INTRODUCTION

This small family of peculiar parasitic wasps is rather poorly represented in Australian collections. Little is known of the habits or life histories of the species. The adults are collected usually on *Eucalyptus* regrowth or bred as parasites from tenthredinid (Hymenoptera) puparia collected in the field as late larvae. Raff (1934) has bred specimens of *Taeniogonalos* as primary parasites of *Perga dorsalis* Leach and *Perga memoralis* Wilson along with primary tachinid and ichneumonid parasites.

These wasps are of rather stout build and have the apex of the abdomen downturned, particularly in the female. They have divided trochanters and many-segmented antennae as in Ichneumonidae but have the ovipositor issuing from the end of the abdomen. Only seven species have been described from Australia, but two of these are considered to be synonyms. A further six species are described, making 11 known species for the Australian fauna. There are five species in *Taeniogonalos* and six in *Mimelogonalos*. One species of *Taeniogonalos* has been collected from Brisbane, Qld., to Bright, Vic. A second, rather similar species, occurs in Tasmania. The third, very differently coloured species, ranges from the Brisbane area north to Kuranda; the fourth is known from Wollongong, N.S.W.; while the fifth was described from Cairns, Qld. *Mimelo-*

---

* Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

gonalos is widespread and all the species are of similar general appearance. There are two species recorded from Tasmania, one from Victoria, two from the A.C.T., and one rather common, smaller species from Brisbane.

Family **TRIGONALIDAE**

Genus MIMELOGONALOS Schulz

Mimelogonalos Schulz, 1907, Gen. Insect. fasc. 61: 8.

Genotype *Mimelogonalos bouvieri* Schulz, 1907, loc. cit., 8 (original designation).

Antenna with scape, pedicel, and 20-23 funicle segments, gradually tapering to the apex, "tyloides" present in male, but variable in number. Hind trochanters 3-segmented, fore and middle 2-segmented. Scutellum with a distinct median longitudinal sulcus. Abdomen ventrally unarmed, convex both above and below; 1st segment of abdomen widening rapidly, wider than long; posterolateral margins of abdominal segments not produced.

The genus, as at present known, is restricted to Australia and Tasmania.

Key to Species of the Genus Mimelogonalos

1. Postscutellum marked with yellow. (Abdomen all black; hind femur all yellow; antenna with 21 funicle segments (♀)) .... *minuta* (Rayment)
Postscutellum entirely black 2
2. Abdomen all black. (Only extreme apex of hind femur black; antenna with 22 funicle segments (♂); tyloides on 7-13 (♂); scutellum marked with yellow) .. *nigricauda*, sp. nov.
Abdomen with segment 2 yellow laterally 3
3. Scutellum all black. (Antenna with 23 funicle segments (♀); apical two-thirds of hind femur black; basal two-thirds of fore femur black) .. *nigrithorax*, sp. nov.
Scutellum marked with yellow 4
4. Antenna with 21 funicle segments (♀); scape laterally considerably longer than wide; segment 2 of abdomen narrowly glabrous at meson .. *partiglabra*, sp. nov.
Antenna with 23 funicle segments in ♀ and 22 in ♂; scape laterally only slightly longer than wide; segment 2 of abdomen finely punctate across meson .... *punctulata*, sp. nov.
Antenna with 20 funicle segments (♀); scape laterally subquadrate; segment 2 of abdomen narrowly glabrous at meson over anterior half ...... *bouvieri* Schulz

Mimelogonalos minuta (Rayment)

Taeniogonalos minutus Rayment, 1952, Vict. Nat. **69**: 94.

The species is redescribed from both sexes.

Female

Black species marked with yellow. Antenna all dark. Face with clypeus and mandibles, except teeth, yellow. Scutellum yellow discally, postscutellum yellow mesally (quite small area) otherwise dorsal thorax black; a small yellow area laterally just below tegula. Abdomen all black. Legs yellow and blackish, mostly yellow. Coxae all black, trochanters all yellow. Fore femur black over basal third, less so above, otherwise yellow; middle femur black over basal two-thirds, less so above, otherwise yellow; hind femur all yellow except for a minute darkening above at apex. Fore and middle tibiae yellow, hind tibia somewhat darkened. Tarsi brownish but with basal segments of fore and middle tarsi lighter. Wing very slightly infuscated at apex.

Antenna with scape, pedicel, and 21 funicle segments. Scape laterally only slightly longer than wide. Head punctate widely around ocelli. Propodeum finely foveate. Segment 2 of abdomen above finely, closely punctate except narrowly at anterior and posterior borders. Femoral furrow coarsely cross-rugose anteriorly below, coarsely irregularly punctate anteriorly above, narrowly glabrous behind.

Male

As female but differing as follows. Legs paler; femora, tibiae, and tarsi marked with reddish brown, not black, hind tarsus darker; hind femur yellow, except apical quarter; wing clear; scape and pedicel red, flagellum dark.

Antenna with scape, pedicel, and 23 funicle segments.

Types.—Holotype ♂ in the National Museum, Melbourne; allotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Holotype, Queensland, Mt. Tambourine (27.i.1950, C. Oke); allotype, Queensland, National Park (20.x.1923, H. Hacker).

Locality records.—QUEENSLAND: Sunnybank (10.x.1930, G. H. Hardy); Brisbane (7.xi.1917, H. Hacker).

In one specimen from Sunnybank the yellow mark on the postscutellum is very indistinct but there is a yellowish brown coloration. This species is distinctly smaller than the others of the genus. The yellow postscutellum, black abdomen, and rather small size are the chief characteristics of the species.

MIMELOGONALOS NIGRICAUDA, sp. nov.

Plate 1, Fig. 5

Male

Black species marked with yellow. Antenna all dark. Face with clypeus and mandibles, except teeth, yellow. Scutellum yellow discally, otherwise thorax black above; a yellow area laterally just below tegula (pronotum). Abdomen entirely black. Legs yellow and black. Coxae all black, trochanters all yellow. Fore femur black over basal third, otherwise yellow; middle femur black over basal half except above, otherwise yellow; hind femur yellow except for extreme apex, which is black. Fore tibia yellow, middle and hind tibiae brown-black. Tarsi dark, but fore tarsus with basal segments lighter. Wing slightly infuscated, more so at apex.

Antenna with scape, pedicel, and 22 funicle segments. Tyloides present on funicle segments 7-13 and slightly on 14. Scape, laterally, only slightly longer than wide. Head almost glabrous around ocelli. Propodeum finely foveate even laterally. Segment 2 of abdomen above finely punctate except narrowly at anterior and posterior borders, but more so at meson, particularly anteriorly.

Femoral furrow of mesothorax coarsely cross-rugose over most of its surface, except posteriorly in middle, and there glabrous.

Type.—Holotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Hobart, Tas. (4.x.1914, G. H. Hardy).

There is a second specimen from the same locality, agreeing with this type, in the Queensland Museum. The species is characterized by the black abdomen and yellow scutellum otherwise with the dorsal thorax black.

MIMELOGONALOS NIGRITHORAX, sp. nov.

Plate 1, Fig. 6

Female

Black species marked with yellow. Antenna all dark. Face with clypeus and mandibles, except teeth, yellow. Dorsal thorax all dark above; a yellow area laterally just below tegula. Abdomen with a large yellow patch laterally on segment 2, otherwise black. Legs black and yellow. Coxae all black, trochanters all yellow. Fore femur black over basal two-thirds, less so above, otherwise yellow; middle femur all black; hind femur black, except for yellow at extreme base. Fore tibia brownish, middle and hind tibiae black. Tarsi black but basal segments of fore tarsus lighter. Wing slightly infuscated, more so at apex.

Antenna with scape, pedicel, and 23 funicle segments. Scape, in lateral view, only slightly longer than wide. Head almost glabrous around ocelli. Propodeum cross-rugulose at meson, otherwise finely foveate. Segment 2 of abdomen above very finely punctate except narrowly at anterior and posterior borders, but more so at meson anteriorly. Femoral furrow of mesothorax coarsely cross-rugose except over posterior third above.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—A.C.T., Mount Gingera (15.i.1950, I. F. B. Common).

The black dorsal thorax is characteristic of this species.

MIMELOGONALOS PARTIGLABRA, sp. nov.

Plate 1, Fig. 4

Female

Black species marked with yellow. Antenna all dark. Face with clypeus and mandibles, except teeth, yellow. A minute yellow spot at vertex of head. Scutellum yellow discally, otherwise thorax black above; a yellow area laterally just below tegula. Abdomen with a large yellow patch laterally on segment 2, otherwise black. Legs black and yellow. Coxae all black, trochanters all yellow. Fore femur with the basal half black; otherwise yellow; middle femur all black; hind femur with the basal third yellow, remainder black. Fore tibia brownish, middle and hind tibiae black. Tarsi black but basal segments of fore tarsus lighter. Wing slightly infuscated, more so at apex.

Antenna with scape, pedicel, and 21 funicle segments. Scape laterally considerably longer than wide, but not twice. Head almost glabrous around ocelli. Propodeum finely foveate. Segment 2 of abdomen above rather coarsely, widely, punctate except at meson, and there narrowly glabrous, connecting the narrow glabrous anterior and posterior borders. Femoral furrow of mesothorax coarsely cross-rugose anteriorly below, irregularly coarsely punctate anteriorly above, glabrous posteriorly.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—A.C.T., Blundells (20.xi.1934, W. Rafferty).

The species has yellow marks on the abdomen and yellow scutellum as in the following species, *punctulata.* In a second female from Tubrabucca Creek, N.S.W. (10-23.i.1948, R. T. M. Pescott and A. N. Burns) in the National Museum, Melbourne, the vertex of the head is all black, the third abdominal segment has a very small yellow area laterally, and the median glabrous area of the second abdominal segment is distinct only over the anterior half.

MIMELOGONALOS PUNCTULATA, sp. nov.

Female

Black species marked with yellow. Antenna all dark. Face with clypeus and mandibles, except teeth, all yellow. Scutellum yellow discally, otherwise thorax black above; a yellow area laterally just below tegula. Abdomen with a large yellow patch laterally on segment 2, otherwise black. Legs yellow and black. Coxae all black, trochanters all yellow. Fore femur black over basal half, less so above, yellow over apex; middle femur all black; hind femur yellow over basal half or so, black at apex. Fore tibia yellow, middle and hind tibiae brown-black; tarsi dark but fore tarsus lighter on basal segments. Wing slightly infuscated, more so at apex.

Antenna with scape, pedicel, and 23 funicle segments. Scape, laterally, only slightly longer than wide. Head rugulose around ocelli. Propodeum finely foveate, anterolaterally rugulose. Segment 2 of abdomen above finely closely punctate, except narrowly at anterior and posterior borders, but more so at meson. Femoral furrow of mesothorax coarsely cross-rugose over anterior half, glabrous behind.

Male

Colouring similar to that of female except that yellow of the scutellum is reduced to a median triangle with apex anterior.

Antenna with scape, pedicel, and 22 funicle segments (one less than in female). Tyloides on funicle segments 8-13. Head more punctate than rugulose. Propodeum similar to female. Segment 2 of abdomen similar but narrowly glabrous at meson over anterior half. Femoral furrow coarsely punctate anteriorly, glabrous behind.

Types.—Holotype ♀, allotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Holotype, Victoria, Lorne (30.xi.1917, F. E. Wilson); allotype, N.S.W., Sawpit Creek, Mount Kosciusko (11.xii.1931, A. L. Tonnoir), 4500 ft.

This species has similar body markings to the preceding species, *partiglabra,* but differs in the coloration of the legs and more definitely in the ornamentation of the abdomen, shape, and number of antennal segments. It is rather close to *bouvieri.*

MIMELOGONALOS BOUVIERI Schulz

Mimelogonalos Bouvieri Schulz, 1907, Gen. Insect. fasc. 61: 8.

The species is redescribed from a female specimen from Cradle Mt., Tas.

Female

Black species marked with yellow. Antenna all dark. Face with clypeus and mandibles, except teeth, all yellow. Scutellum yellow discally, otherwise thorax black above; a yellow area laterally just below tegula. Abdomen with a yellow patch laterally on segment 2, otherwise black. Legs yellow and black. Coxae all black, trochanters all yellow. Fore femur black over the basal half or so, yellow at apex; middle femur all black; hind femur yellow over more than the basal half, black at apex. Fore tibia yellow, middle and hind tibiae brown-black; tarsi dark but fore tarsus lighter on basal segments. Wing slightly infuscated, more so at apex.

Antenna with scape, pedicel, and 20 funicle segments. Scape laterally almost quadrate. Head rugulose around the ocelli. Propodeum foveate, anterolaterally rugulose. Segment 2 of abdomen above finely, closely punctate, except narrowly at anterior and posterior borders and narrowly at meson over anterior half. Femoral furrow of mesothorax coarsely cross-rugose over anterior half, glabrous behind.

Type.—Holotype ♀ apparently lost. Not in the Paris Museum.

Type locality.—Tasmania.

There is a second female from Cradle Mt., Tas., in the Division of Entomology, C.S.I.R.O. The species differs markedly from *nigricauda,* also of Tasmania, in the coloration of the legs and abdomen.

Genus TAENIOGONALOS Schulz

Taeniogonalos Schulz, 1907, Gen. Insect. fasc. 61: 15.

Genotype *Trigonalys maculata* Smith, 1851, Ann. Mag. Nat. Hist. (2) 7: 28 (here designated).

Schulz did not designate a genotype. I here designate *maculata* Smith 1851, the earliest described species, as genotype and rediagnose the genus as follows:

Antenna with scape, pedicel, and 20-24 funicle segments, gradually tapering to a fine point, "tyloides" present in male, but variable in number. Hind trochanter 3-segmented, fore and middle 2-segmented. Scutellum with a distinct median longitudinal sulcus. Abdomen below, in female, armed with a large backwardly directed spine from at least the 2nd segment (spine absent in male); 1st segment of abdomen small, not nearly as wide as 2nd; segment 2 of abdomen above slightly concave at meson (only very slightly so in some species); posterolateral margins of abdominal segments not produced; abdomen convex below.

KEY TO AUSTRALIAN SPECIES OF THE GENUS TAENIOGONALOS

1. Antenna all black. (Ventral process from 3rd abdominal segment (♀) distinctly bifid at apex; antenna with 22 funicle segments) (♀)...... *tenebrosa*, sp. nov.
   Antenna reddish brown in part.. 2
2 Wing deeply infuscated only anteriorly.................................. 3
   Wing evenly infuscated. (Third abdominal segment (♀) without process ventrally) (♀)................................ *semibrunnea* (Bischoff)
3. Species mostly black. (Antenna with 22 to 24 funicle segments; 3rd abdominal segment (♀) with only a very slightly produced carina ventrally; "tyloides" in (♂) antenna on funicle segments 7-12 or 13) (♂, ♀).... *maculata* (Smith)
   Species strongly marked with yellow or yellow and red.................... 4
4. Female with process from 2nd abdominal segment slightly bifid at apex, 3rd segment with a lamellate process; antenna with 23 funicle segments (♀)........ *tricolor* Rayment
   Female with process from 2nd abdominal segment entire at apex, 3rd segment without process; antenna with 24 or 23 funicle segments (♀).............. *tricolor similis*, subsp. nov.
   Female with process from 2nd abdominal segment slightly bifid at apex, 3rd segment with a triangular-sided process; antenna with 20 funicle segments (♀).. *chadwicki*, sp. nov.

TAENIOGONALOS MACULATA (Smith)

Plate 1, Fig. 1

Trigonalys maculata Smith, 1851, Ann. Mag. Nat. Hist. (2) **7**: 28.
Taeniogonalos maculata Schulz, 1907, Gen. Insect. fasc. **61**: 15.
Taeniogonalos heterodoxus Rayment, 1948, Aust. Zool. **11**: 241.
Taeniogonalos heterodoxus Rodd, 1951, Aust. Zool. **11**: 338.
Taeniogonalos heterodoxus Rayment, 1951, Aust. Zool. **11**: 340.
Taeniogonalos burnsi Rayment, 1952, Vict. Nat. **69**: 94.

Female

Black species marked with yellow and reddish brown. Antenna reddish brown, except for apical half of funicle and middle of scape, less so pedicel and 1st funicle. Face black, marked with yellow; clypeus with yellow patch under each antenna, mandible yellow except for teeth and laterally, small yellow patch bordering insertion of antenna above and laterally to eye and there expanded; border to the lateral margin of the eye distinctly yellow; posterior border of the head narrowly yellow, except at meson. Thorax mostly black, scutum with small yellow patch at anterolateral corner, smaller patch on axilla discally, postscutellum laterad and propodeum at posterolateral border yellow. Abdomen above black, with distinct transverse yellow bands, 1st segment with apical half yellow, 2nd with an equally wide yellow band just before apex, 3rd all black, 4th similar to 2nd but much smaller, 5th mostly yellow, except basally, 6th mostly yellow, except mesally. Legs mostly reddish brown, femora darkened at bases, coxae all black, trochanters all marked with yellow, fore trochanter with basal segment with a black cinctus in middle, broken below, apical segment yellow, middle trochanter similar to fore but cinctus complete, hind trochanter with the 3 segments all yellow.

Antenna with scape, pedicel, and 24 funicle segments, the apical 2 sometimes indistinctly divided. Third segment of abdomen ventrally with only a very slightly produced transverse ridge. Fore wing deeply infuscated over the anterior half.

The trochanters may be darker with even the hind trochanter showing some black and the antenna may have scape, pedicel, and 1st funicle segment dark.

Male

Differs somewhat in coloration. Antenna all reddish brown at base, apex of flagellum slightly darkened. Mesothorax with small yellow areas extending from tegula to anterolateral scutum and just above fore coxa anteriorly. Small yellow patch on scutellum posteromesally from patch on axilla. Trochanters all marked with reddish brown, fore trochanter with cinctus of basal segment broken above and below.

"Tyloides" on funicle segments 7-12 or 13. Antenna with 23 funicle segments, sometimes reduced to 22.

In a male from Blackheath, the antenna is coloured as in the female, the mandible has more yellow laterally, the yellow at the vertex of the head is very indistinct, the axilla, scutellum, and propodeum are all black above, the mesothorax as in the description above but with the anterior border above narrowly yellow, the abdomen with the yellow bands reduced, 1st segment with yellow distinct, 2nd segment with yellow band narrow and broken at meson, yellow of 4th segment reduced, that of 5th normal, 6th with more yellow, and "tyloides" on segments 7-13 and slightly so on 14.

Type.—Holotype ♂ (considered ♀ by Schulz 1907) in the British Museum. The types of *heterodoxus* Rayment are in the T. Rayment collection. The holotype of *burnsi* is in the A. N. Burns collection.

Type locality.—Queensland, Moreton Bay.

Locality records.—AUSTRALIAN CAPITAL TERRITORY: Canberra (14.iv.1947, E. F. Riek), 1 ♀ bred from puparium of tenthredinid, *Perga dorsalis* ? Leach, collected as a late larva; Blundells (7.iii.1934, W. Rafferty), 1 ♀.

NEW SOUTH WALES: Blackheath (21.xi.1919, G. H. Hardy); 1 ♂.

VICTORIA: Heathmont (16.iv.1946, A. N. Burns); Ferntree Gully (Feb. and Apr. 1932, A. N. Burns).

The antenna of the holotype of *maculata* must have been broken at the tip, thus accounting for the statement that the antenna was 19-segmented. Rayment separated the form occurring near Sydney on very slight colour differences and based the species *burnsi* on a rather dark specimen from near Cobungra, Vic.

There is considerable variation in the colour markings. The yellow mark on the axilla and scutellum is sometimes reduced or absent and the propodeum is occasionally all dark, but at other times may show a pair of rather large yellow areas. The vertex of the head is rarely all dark in females but is more often so in males. The yellow bands on abdominal segments 4-6 are usually joined across the meson. There are some constant variations between populations. In a series of five bred males from Heathmont, Vic. (16.iv.1946, A. N. Burns), the propodeum has a pair of large yellow spots, whereas in a series of 20 specimens (11 ♂♂, 9 ♀♀) from Ferntree Gully, Vic. (Feb.-Apr. 1932, A. N. Burns), the propodeum is always dark in the male and occasionally so in the female, and even when present, the yellow marks are small.

In the holotype of *burnsi* Rayment the dorsal thorax is nearly all dark, except for a small spot laterally on postscutellum and a minute spot anterolaterally on the scutum. The vertex of the head has only a pair of minute spots. The trochanters are dark but the fore and hind trochanters are pale above.

TAENIOGONALOS TENEBROSA, sp. nov.

Plate 1, Fig. 3

Female

Black marked with whitish yellow and reddish brown. Antenna all black. Face mostly black, clypeus laterally with small whitish patch, mandible whitish except for teeth and laterally, small whitish patch on mesal border of eye at level of antennal insertion, distinct whitish zone bordering all the lateral margin of the eye. Thorax mostly black, scutum with small yellowish patch at anterolateral corner, smaller patch on axilla discally, similar patch on scutellum laterally, almost touching that of axilla, small patch on postscutellum laterally, distinct area on mesothorax laterally from below tegula to anterolateral corner of scutum. Abdomen above with distinct transverse yellowish bands, almost apical half of 1st segment yellowish, band of similar width almost at apex of 2nd segment, 3rd segment black, 4th segment yellowish over the apical half, more so at meson, 5th mostly yellow. Legs reddish brown, femora very slightly darkened at bases, tarsi darkened at apices, coxae all black, all trochanters yellow, marked with black, basal segment of all 3 trochanters with black in middle, that of fore and middle trochanters broken above, that of hind trochanter broken above and below, apical segment of fore and middle trochanters and apical 2 segments of hind trochanter yellow.

Antenna with scape, pedicel, and 22 funicle segments. Abdomen with distinct backwardly directed ventral projections from segments 2 and 3. that from 3 only half the length of that from 2 and both obviously bifid at apex, that from 3 very narrow and blade-like when viewed laterally. Fore wing deeply infuscated along the anterior border, particularly beyond the pterostigma where it also extends more posteriorly.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Tasmania, Westerway (21.i.1949, E. F. Riek).

This species differs from the mainland *maculata* in its slightly different coloration, notably of face and antenna, in the reduced number of segments in the antenna, and in the shape of the ventral process from the third segment of the abdomen.

TAENIOGONALOS TRICOLOR Rayment

Plate 1, Fig. 2

Taeniogonalos tricolor Rayment, 1952, Vict. Nat. **69**: 96.

TAENIOGONALOS TRICOLOR TRICOLOR Rayment

Female

Black and yellow species, strongly marked with yellow. Antenna reddish brown, except for middle of scape and apical half of funicle, which are black. Face below antennal insertion nearly all yellow, clypeus yellow, with median black spot below, mandible yellow except for teeth and laterally over part of base, yellow around antennal insertion and laterally to eye, there bordering the mesal margin, lateral margin of the eye widely bordered with yellow, small yellow spot below median ocellus and smaller one at lateral margin of lateral ocellus, posterior border of head with irregular yellow band. Thorax with much yellow, small patch on anterolateral border of scutum, most of axilla, scutellum, except mesally and posteriorly, most of postscutellum except posteriorly and there reddish brown, propodeum except medianly (widely so) and anteriorly yellow, thorax laterally mostly black except from below tegula widely to anterolateral scutum, small patch just above fore coxa and mesothorax mesally at anterior border narrowly. Abdomen above with 1st segment all yellow, 2nd yellow over distal third, 3rd similar but not as distinctly yellow, 4th and 5th nearly all yellow except for anterior border. Legs reddish brown, all coxae black at base, yellow at apex, trochanters all yellow and all tibiae yellow at base.

Antenna with scape, pedicel, and 23 funicle segments. Second segment of abdomen below produced into a distinct process, bifid at apex, 3rd segment with slightly produced but distinct carina or plate, with entire margin. Fore wing deeply infuscated along the anterior border, more particularly so beyond the pterostigma.

There is some variation in the one series of specimens in the yellow coloration, some of the zones uniting to give larger areas or else reduced and so more widely separated, but the colour centres are as indicated in the above description.

Male

Antenna all reddish brown, a little darkened at apex. Head marked with yellow as in the female. Thorax with scutellum and postscutellum all yellow. Legs with only extreme bases of coxae black, otherwise light reddish brown, trochanters not obviously yellow.

Abdomen below without processes but with a very slight tubercle on segment 2. Antenna with "tyloides" on segments 7-12.

Types.—Holotype ♀ in the A. N. Burns collection, allotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Holotype, Queensland, Kuranda (15.xi.1951, A. N. Burns); allotype, Brisbane (Feb. 1944, E. F. Riek).

Locality records.—QUEENSLAND: Brisbane; Mt. Tambourine (1916, Davidson); Stradbroke I. (17.ix.1915, H. Hacker); Magnetic I. (9.i.1946, O. W. Sturgess); Mt. Gravatt (8.i.1928, A. N. Burns).

This is a very distinct species with much yellow coloration, appearing, in general, more yellow than black. The specimens from Brisbane were collected on or flying near eucalypt regrowth during the summer months.

TAENIOGONALOS TRICOLOR SIMILIS, subsp. nov.

Female

Colouring as in *tricolor* but the apical pale band of the 3rd abdominal segment wide and distinct. Antenna all dark or pale over the basal flagellum.

Ventral process from the 2nd abdominal segment entire at apex, i.e. not bifid but truncate; 3rd abdominal segment without process ventrally, antenna with 24 funicle segments or with 23 and an elongated apical segment as in the holotype.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Two paratype females in the A. N. Burns collection.

Type locality.—Queensland, Magnetic I. (9.i.1946, O. W. Sturgess).

Locality record.—QUEENSLAND: Brisbane (21, 27.ii.1928, A. N. Burns), bred from sawfly.

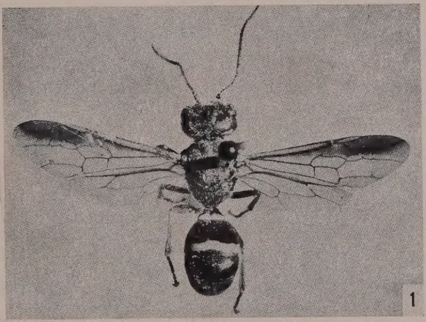
TAENIOGONALOS CHADWICKI, sp. nov.

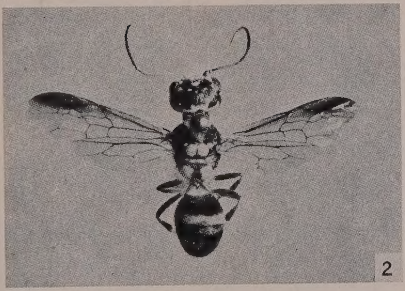
Female

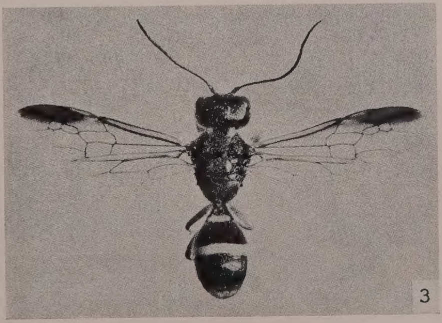
Black and red species with some yellow markings, particularly on face and abdomen. Antenna yellowish, reddish brown over apical half. Face below antennal insertions nearly all yellow, clypeus yellow, with median black zone particularly below, mandible yellow except for teeth and at base in part, yellow at antennal insertion laterally and laterally to eye, there bordering the mesal margin, lateral margin of the eye widely bordered with yellow; dorsal surface of head all reddish except for small black spots at lateral ocelli and larger black area above antennal insertion. Thorax above marked with red and yellow, propodeum mostly black; yellow at anterolateral scutum, pronotum laterally above, a small spot on each side of postscutellum, and a very small spot on each side towards caudal margin of propodeum; red at all scutellum and postscutellum, except for yellow spots, axilla and at parapsidal groove over caudal half; lateral and ventral thorax all black. Abdomen above with 1st segment all yellow, 2nd yellow over distal third except for black caudal margin, 3rd all dark, 4th, 5th, and 6th yellow widely at meson; abdomen below yellow at apex narrowly and posterolaterally of 1st segment and posterolaterally of 2nd and produced area at meson. Legs reddish brown, all coxae black, narrowly pale at apices, hind trochanter all yellow, middle and fore trochanters dark anteriorly and posteriorly.

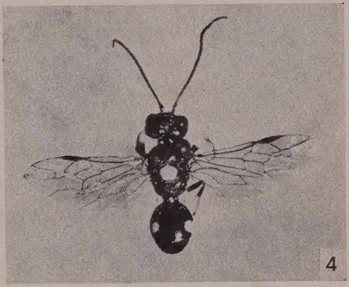
Antenna with scape, pedicel, and 20 funicle segments, the apical segment slightly longer than the penultimate. Second segment of abdomen below produced into a distinct process, clearly bifid at apex, 3rd segment slightly produced at meson into a triangular point by the meeting of the 2 lateral carinae and

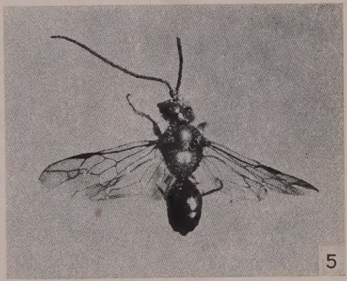
AUSTRALIAN TRIGONALIDAE


1


2


3


4


5

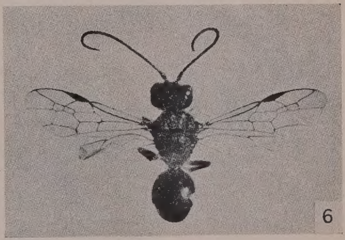

6

Fig. 1.—*Taeniogonalos maculata* (Smith), ♀, specimen from Blundells, A.C.T. × 3.
Fig. 2.—*Taeniogonalos tricolor* Rayment, ♀, specimen from Brisbane, Qld. × 3.
Fig. 3.—*Taeniogonalos tenebrosa*, sp. nov., ♀, holotype from Westerway, Tas. × 3.
Fig. 4.—*Mimelogonalos partiglabra*, sp. nov., ♀, holotype from Blundells, A.C.T. × 3.
Fig. 5.—*Mimelogonalos nigricauda*, sp. nov., ♂, holotype from Hobart, Tas. × 3.
Fig. 6.—*Mimelogonalos nigrithorax*, sp. nov., ♀ holotype from Mt. Gingera, A.C.T. × 3.

a median longitudinal carina. Fore wing deeply infuscated along the anterior border, more particularly so beyond the pterostigma.

Type.—Holotype ♀ in the Entomological Branch collection of the New South Wales Department of Agriculture, Sydney.

Type locality.—N.S.W., Wollongong (8.vi.1947, C. E. Chadwick).

Only the holotype is known. The species has most distinctive abdominal processes and antennal segmentation. The colouring too differs quite markedly from *tricolor* to which it is most allied.

TAENIOGONALOS SEMIBRUNNEA (Bischoff)

Lycogaster semibrunnea Bischoff, 1951, Ann. Mag. Nat. Hist. (12) **4**: 912.

Bischoff stated that the antenna is very long and tapering and is without thickening in the middle. This type of antenna occurs in *Taeniogonalos,* not in *Lycogaster.* He examined only the female holotype. The colouring, particularly of the abdomen, is distinctive. The evenly infuscated wing further separates it from the other Australian species.

Type.—Holotype ♀ in the British Museum.

Type locality.—Queensland, Cairns (1912, Turner).

REFERENCES

Bischoff, H. (1951).—Ueber einige Trigonaloiden des British Museum. *Ann. Mag. Nat. Hist.* (12) **4**: 908-14.

Raff, Janet W. (1934).—Observations on sawflies etc. *Proc. Roy. Soc. Vict.* **47**: 54-77.

Rayment, T. (1948).—Notes on remarkable wasps and bees. *Aust. Zool.* **11**: 238-54.

Rayment, T. (1952).—New bees and wasps. xvii. Rare parasitic wasps. *Vict. Nat.* **69**: 93-9.

Rodd, N. W. (1951).—Notes on the biology of an Australian trigonalid wasp. *Aust. Zool.* **11**: 338-40.

Schulz, W. A. (1907).—"Trigonalidae" *in* "Genera Insectorum." fasc. 61.

Smith, F. (1851).—*Ann. Mag. Nat. Hist.* (2) **7**: 28.

LIST OF SPECIES

Genus *Mimelogonalos*		Genus *Taeniogonalos*	
M. bouvieri Schulz	301	*T. chadwicki,* sp. nov.	306
M. minuta (Rayment)	297	*T. maculata* (Smith)	302
M. nigricauda, sp. nov.	298	*T. semibrunnea* (Bischoff)	307
M. nigrithorax, sp. nov.	299	*T. tenebrosa,* sp. nov.	304
M. partiglabra, sp. nov.	299	*T. tricolor* Rayment	305
M. punctulata, sp. nov.	300	*T. tricolor similis,* subsp. nov.	306
		T. tricolor tricolor Rayment	305